Univerzita Karlova v Praze

Přírodovědecká Fakulta

Studijní program: Biologie

Studijní obor: Ekologie

Studijní zaměření: Terestrická ekologie

Bc. Hana Dlouhá

Vztah mezi škálováním diverzity a počtem jedinců ve společenstvu

Diplomová práce

Školitel: prof. RNDr. David Storch, Ph.D.

Praha 2013

Charles University in Prague

Faculty of Science

Study programme: Biology

Master study of Ecology

Curriculum of Terrestrial Ecology

Bc. Hana Dlouhá

The relationship between spatial scaling of diversity and the number of individuals

Master thesis

Supervisor: prof. RNDr. David Storch, Ph.D.

Prague 2013

Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, 15.8.2013

Acknowledgement

If you read these lines printed on paper it means that I have completed so far the most demanding quest in my life. And I am really grateful for that simple fact. So I would like to write down few notes about important people in my recent life.

Firstly and mainly my thanks belong to my understanding supervisor who came up with the topic in the first place and gave me plenty of recommendations and guidelines. Further I am grateful for the support, amusement and sometimes even silence I found in the workroom for students of ecology where most of this work has been written. I am also thankful to Petr Keil and Louskáček for valuable advices concerning mainly statistical analyses and to Pavel for reading the whole work and reminding me of all the mistakes I did not noticed.

Last but not least I would like to express my thanks towards my family and to Michal. I am completely aware that without your support I would not be able to finish my studies. Mum, please, translate it to dad!

Thank you all!

Abstrakt

Zákonitosti spojené s nárůstem počtu druhů při zvětšování zkoumané plochy (tzv. *species-area relationship*, SAR) patří již dlouho mezi nejstudovanější témata v ekologii. Nejprve převládaly studie zaměřující se na dílčí SAR křivky založené na studování jediné, popř. několika málo lokalit. Poslední dobou se ale začaly objevovat i sjednocující přístupy, které se snaží zobecňovat a hledat nové unifikující rámce pro species-area relationship. Jeden ze směrů se zabývá vztahem mezi průměrnou druhovou abundancí (N/S) a rychlostí přirůstání druhů se vzrůstající plochou (sklon SAR křivky). Podle této teorie vede vyšší počet jedinců připadajících průměrně na druh k nižším sklonům SAR křivky. Na základě těchto úvah vznikla i predikce založená na maximalizaci entropie (MaxEnt), která je schopna konkrétním hodnotám N/S přiřadit hodnotu sklonu SAR křivky.

Hlavním cílem mé práce bylo shromáždit co nejširší datovou základnu zahrnující data o sklonech SAR křivek a průměrných druhových abundancích k nim náležejícím. Do následujících analýz jsem zahrnula i další proměnné a snažila jsem se o stanovení jejich významu pro predikování sklonu SAR křivky. Analýzy, které jsem prováděla, můžeme rozdělit do dvou hlavních skupin, analýzy celkového a lokálního sklonu SAR křivky. Nejprve jsem se zaměřila na celkový sklon (sklon výsledné přímky v lineární regresi), jeho nejlepší prediktory a úspěšnost MaxEnt predikce. Přestože tato predikce byla původně určena pro lokální sklony, vysvětlila 54% z celkové variability hodnot pro celkové sklony. Nejvlivnějšími proměnnými pro celkové sklony se ukázaly *průměrná druhová abundance* (jejíž vliv byl nelineární), kategorická proměnná *organismus* a *rozsah ploch*, přes který byla konstruována SAR křivka. U analyzování lokálních sklonů MaxEnt přístup neprokázal tak velkou prediktivní schopnost a vysvětlil pouze 0,93 % z celkové variability. Průměrná druhová abundance se neukázala jako významný prediktor ani při analyzování lokálních sklonů jako takových (při hledání jejich nejvlivnějších prediktorů). Naopak jako proměnné s největším vlivem na lokální sklony byly vyhodnoceny kategorická proměnná *organismus*, *střední hodnota zeměpisné šířky* a *plocha*, na které byl lokální sklon vypočítán a která nás ukotvuje na SAR křivce.

Průměrná druhová abundance je zřejmě velmi důležitým prediktorem pro celkové sklony SAR křivky, nicméně její vliv na lokální sklony SAR křivky je zanedbatelný.

Klíčová slova: species-area relationship, SAR, biodiverzita, průměrná druhová abundance, makroekologie

Abstract

The patterns connected with increasing number of species while enlarging studied area (species-area relationship, SAR) remained one of the most studied topics in ecology. In the past, papers presenting single SAR curves prevailed. Recently, also unifying works have appeared. One approach has focused on the possible relationship between mean number of individuals per species and the rate of increase of number of species with area. According to this theory higher mean species abundance leads to lower values of SAR curve slope. Moreover, there is one prediction based on maximization of entropy principle (MaxEnt) that is able to give us particular values of SAR's slope when we provide the values of mean species abundance. There are also other approaches except for MaxEnt one that deals with mean species abundance and reached similar results.

The main aim of this work was to gather all possible data about slopes of SARs and mean species abundances and find out possible relationships between these two variables. I have also included several other variables into the analyses to reveal the importance of them as predictors for the values of the slope. I performed two main groups of analyses. At first I focused on overall slopes of SAR curve (overall slope represents the slope of a line that resulted from linear regression applied to the data points), its predictors and the quality of MaxEnt prediction. MaxEnt approach (even if it was designed for local slopes) was able to explain 54% of variability in overall slope values. The most influential variables for overall slopes happened to be mean species abundance, its quadratic term, organism area range that encompass the information about the area span in original paper. As for the local slopes MaxEnt prediction did not suit the data very well and it was able to explain just 0.93% of variability in the slope. Mean species abundance was not revealed as a significant and influential predictor in the analysis of local slope values. Variables with the highest impact on local slope values were organism, latitude midpoint and focal area (particular area size that is connected with local slope value).

As there is distinctive impact of mean species abundance on overall values, surprisingly its affect on local slope values is minor.

Key words: species-area relationship, SAR, biodiversity, mean species abundance, macroecology

Contents

1. Aims of my work

Besides the general introduction that directly follows after this section I would like to summarize its content with accent on the aims of my work. This section therefore includes some information that is also included in the next chapter. Still I wanted to outline main ideas and issues that are fundamental for my thesis. I intentionally omitted references (please, seek for them in following chapter) to preserve the clarity of this chapter.

The change in species composition and their diversity in space have been attaching scientist's attention for a long time. One option how to measure this effect is the *species-area relationship* (abbreviated as SAR), that describes the rate of increase of number of species when enlarging the area. Usually we operate with slopes (z) of SAR curve to enable comparison between different SARs and to quantify the rate of species' increase. A lot of effort was devoted into a search for ideal predictor that might forecast the slope. Originally, variables such as latitude, body mass or characteristics of environment (productivity, island vs. mainland *etc*.) were used to predict z values. Recently unifying tendencies with ambitions to use single predictor encompassing several other characterizations have emerged. My work is focusing on one of them. In particular I wanted to explore properly the relationship between mean species abundance (number of individuals per species) and slope of SAR curve. Few theoretical papers reached similar results that suggest that with increasing mean species abundance the slope of SAR curve decreases. This theory was verified on restricted data sets. Here comes my work with main aim to test these theoretical predictions on wider data sets. Optionally I wanted to study possible mutual relationship between mean species abundance and other predictors, with an ideal result that mean species abundance is able to stand in analyses for some other variables

2. General introduction

2.1. SAR, its shape and basic properties

There is a lot of variation in species distribution on the surface of our planet. This character of our world is evident and a lot of attention has been focused on that. It started with simple descriptive studies, but later on people started to quantify the patterns of distribution and diversity. One way how to express spatial changes of biodiversity is the description of accumulation of species with enlarging area. This relationship is called *species-area relationship* (SAR) and it belongs to the topics that receive major attention in macroecology.

The shape of SAR refers to the differences in composition of species assemblages not only between spatial scales but also between adjacent plots. Steeper slope of SAR is observed when we study some area from fine scale toward coarse scale and involved adjacent areas differ a lot. When we examine adjacent plots in that space we obtain similar picture, considerable turnover in species composition from one location to another. Hence SAR slope also provides information about β diversity (MacArthur 1965; Connor & McCoy 1979). There are also some ways how to calculate exact β-diversity using SAR slope (Ricotta *et al.* 2002).

It is obvious that diversity increases with enlarging area. But the accurate form of SAR, its shape and slope still remain a subject to discuss.

The most frequently used form of SAR is a linear increase in diversity with area that is obtained by transforming both variables to logarithmic scale. This form is based on the power law that Arrhenius came up with (Arrhenius 1921) and it states that $S = c \cdot A^z$, where S represents number of species, A is sampled area, c is taxon specific constant and z is slope of the regression line in log-log space. Main attention is devoted to exponent z as it refers to the rate of increase of species with area. When variables are not logarithmically transformed we need both parameters (c and z) to describe the rate of species increase with area (Connor & McCoy 2001).

Shortly after Arrhenius' paper that involved first mathematical expression of SAR (Arrhenius 1921), another form of expressing SAR in exact way has been proposed. Gleason (1922) discussed the logarithmic increase of diversity with area. Starting with Gleason's paper a lot of studies has assessed other functions to describe more accurately the shape of SAR (Tjorve 2003; Dengler 2009; Tjorve 2009). Basically we can distinguish two major groups of suggested models for fitting the data, concave and sigmoid ones. Most of them are operating with upper asymptotes (Dengler 2009). As Dengler (2009) pointed out the reasons for major usage of power and logarithmic models are not biological but just phenomenological. Other

functions can describe SAR even more precisely with respect to biological processes underlying the SAR. The main advantage of using the power function to fit empirical data is a possibility to compare results of various studies and easily describe the main character of species increase with area (Dengler 2009).

Graphical representation of SAR across wide range of spatial scales suggests that local slopes corresponding to distinct scales vary widely. This basic fact has been recognized several decades ago (Martin 1981). Steep slope could be observed at fine and broad spatial scales whereas intermediate scales exhibit shallow slope (Shmida & Wilson 1985; Rosenzweig 1995; Hubbell 2001), see fig.1. At finest scales SAR appears concave, it follows as a power law at intermediate scales with z usually between 0.1 and 0.25 (Rosenzweig 1995). Finally, as the area expands to coarse grain (entire continents, whole globe) z is no longer constant. The curve exhibits convex behaviour and the exponent z asymptotically increases towards $z = 1$ (Preston 1960; Rosenzweig 1995; Hubbell 2001). Because of this character of SAR it is called triphasic. Supposedly, mechanisms leading to various slopes differ on local, regional and continental scales. Hubbell (2001) suggested major factors influencing local slopes to be relative abundance of species at very local scales and rates of speciation, extinction and dispersal at regional to subcontinental scales. There were also other approaches dealing with intermediate scale slopes. For example Rosenzweig (1995) proposed habitat heterogeneity to be the main driver responsible for power law relationship at intermediate scales. At these spatial scales self-similar species distribution also has been considered (Harte *et al.* 1999; Šizling & Storch 2004). Finally, according to Hubbell (2001) a crossing over major dispersal barriers leads to higher slope at intercontinental scale. The main factors leading to triphasic shape of SAR are relative species abundances, spatial structure within the range and range size limitation at finest, intermediate and coarse scales, respectively.

We should take into consideration the triphasic character of SAR while fitting empirical data with some function. The slope really depends on the area range (Allen & White 2003) and on the spatial scale (Palmer & White 1994). Therefore power law fitting does not have to be the best option to choose, although it might be a good approximation at some scales and we might take advantage of the most widely used form of SAR that allows us to compare large amount of studies.

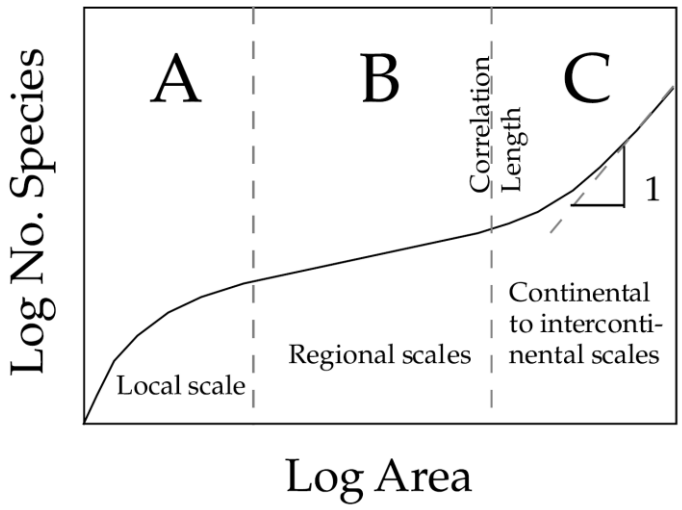

Figure 1 Shape of the species-area relationship across wide range of spatial scales (Hubbell 2001).

There is also some variability in the slope of the SAR within the regions we might distinguish in SAR curve (local slopes within *e.g.* regional scale interval still differs, triphasic curve gives us only basic idea about the steepness of SAR curve in particular intervals). Therefore, a lot of studies concerning the SAR and the factors determining its slope have been published in last several decades (Connor & McCoy 1979; Rosenzweig 1995; Hubbell 2001; Drakare *et al.* 2006). In the past, mainly empirical papers dominated. Recently, theoretical works concerning mathematical aspects of the relationship have appeared. One influencing approach to SAR is based upon self-similarity concept and fractal geometry (Harte *et al.* 1999; Lennon *et al.* 2002; Šizling & Storch 2004; Storch *et al.* 2008). Now this continues with studies that unifies both the attitudes and connects empirical data with theoretical foundations (Harte *et al.* 2009; Šizling *et al.* 2011; Storch *et al.* 2012).

2.2. Processes underlying SAR

What are the mechanisms that lie behind the increase of species richness with area? Generally, these factors differ between island SARs and mainland SARs from continuous areas. I will focus on the mainland situation.

SAR within continuous mainland is determined by factors that set spatial distribution of species. Usually, there are three main mechanisms that are thought to build SAR (Storch *et al.* 2003).

i. *Sampling effect*: since most of species exhibit low abundances (Preston 1948) majority of them is not present in all sampled areas. Even with ideally random

distribution bigger portion of species could be found just in larger areas. Therefore *sampling effect* all by itself is capable of generating monotonically increasing SAR (Preston 1962a). However pure *sampling effect* does not represent sufficient explanation for power law relation nor empirically measured slopes of SAR (Leitner & Rosenzweig 1997).

ii. *Habitat heterogeneity* has been discussed in detail for example by Rosenzweig (1995). The basic idea is simple – larger area contains more types of habitats and thus allows coexistence of more species that are associated with specific habitats. Heterogeneity of habitats then potentially impacts aggregation of species in space. Obviously, spatial aggregation can be influenced by many other factors such as population dynamics or aggregative behaviour. For example truly suitable habitat is not occupied by a species if it is so isolated from surrounding habitats that the probability of colonization remains minimal.

iii. *Spatial population dynamics* is considered to be the third mechanism underlying SAR. Storch *et al.* (2003a) showed that it has conclusive effect on SAR. High dispersal rate generally leads to more homogenous (thence less aggregated) distribution, which corresponds to lower z. And really, dynamic models confirm that higher dispersal corresponds to shallower slope (Rosindell & Cornell 2007). Rosenzweig (1995) also gives credit for the differences between mainland SARs (z between 0.1 and 0.2) and island SARs (z between 0.2 and 0.5) to the dispersal rate. According to the theory of island biogeography (MacArthur & Wilson 1976) islands are occupied by lower number of species than area of the same size on the mainland. There are two major reasons leading to this fact: some species are just not capable to reach these islands and some species are not able to form long-lasting viable populations on these islands. Migration of species to an island is naturally restricted and therefore the extinction is not compensated by the immigration of species.

In general we can conclude that any biological factor or process influencing species distribution in space towards lower aggregation of individuals in space or towards higher homogeneity of species distributions tends to reduce the slope of SAR and conversely, factors leading to enlargement of the dissimilarity between plots and higher aggregation tend to increase the slope of the SAR. Once again there is an obvious linkage between β-diversity and the slope of SAR.

2.3. Experimental design

Experimental design strongly influences the shape of the SAR. We can define two basic dichotomies. First of them deals with possible isolation of a plot by unsuitable environment that does not allow persistence of species population (for example sea that encompass the island). Whether the surrounding habitat is unsuitable obviously depends on the scale we are examining, as unsuitable broader scale plot may comprise suitable smaller habitats. Second differentiation consists in the relationship between smaller and larger plots. *Nested design/ sampling* means that larger plot includes smaller subplots. *Independent design/ sampling* works with spatially non-overlapping plots.

We might distinguish several types within the framework of *nested design* SARs (further distinction covers just mainland nested designs as for nested design on archipelagos there is a lot of options which islands put together and form larger plot) (Storch *et al.* unpublished), see figure 2.

i. *Incomplete nested design* is based on smaller plots that are randomly placed within larger plots and do not fill in these larger plots completely (therefore *incomplete*). Numbers and locations of nested subplots may vary. Mutual relationship between species richness of small subplots and larger plots is influenced by the location of subplots (subplots placed at spots with locally low diversity might lead to bigger difference between richness of subplot and plot than the opposite situation). This design is usually used for constructing SARs for areas with strongly defined borders, such as forested patches or nature reserves.

ii. *Non-overlapping complete nested design* comprises subplots that are not overlapping each other and entirely fill in the area of larger plot (therefore *complete*). This methodological approach is usually used for analyses of gridded biodiversity atlas data where focal scale regions are grouped together in larger regions.

iii. *Overlapping complete nested design* comprises all subplots that can be placed within larger plots (subplots may overlap each other). We might imagine the process of placing the subplots as “moving window” operation.

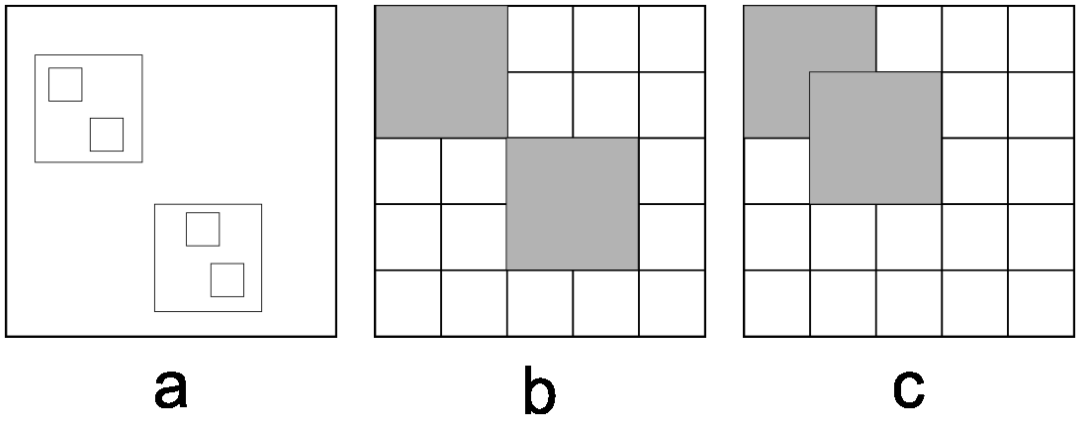

Figure 2 Nested design subtypes; a – incomplete, b – non-overlapping complete, c - overlapping complete, according to Storch *et al.* (unpublished)

Both complete designs bring some constraints for species richness of larger plots via diversity in its subplots. The overlapping design has to be treated for pseudoreplication because of the repeated sampling of spatial points by several plots. Another issue that could influence the results is the fact that areas located in the middle of study area are sampled with higher frequency in comparison to those located on peripheries. On the other hand, the complete overlapping design seems to approximate species richness of randomly located plot within the area most precisely.

I will describe some properties of nested design in more detail as I am mainly dealing with it. Firstly the nestedness of quadrats brings us some information about the species richness. We know that larger plot contains at least all the species that were present in smaller plot. Important condition of using these data is relative homogeneity of this region so that the distribution of species would be relatively random.

The accuracy of SAR also depends on the number of sampled plots and the rate of increase of area. Simple expression of this enlargement between plots is usually marked as ε (epsilon) and refers to the portion of the area of the plot at focal scale to the plot at next coarser scale (Drakare *et al.* 2006).Especially for determining local slopes more measured plots means more accurate result.

In a homogenous environment where all species are randomly distributed, SAR patterns are not dependent on choice of sampling design. However, in nature aggregated distribution of species is observed (Taylor *et al.* 1978, 1979; McArdle *et al.* 1990; Condit *et al.* 2000). That is why choice of a sampling method brings some constraints and influences the final shape of SAR. For example, some sampling methods always lead to non-decreasing relationship (since they deal with increasing numbers of same size quadrats all the time) (Scheiner 2003). On the

contrary, it is possible (at least theoretically) that larger island hosts lower species richness than other, smaller island (we do not have any information about their mutual relationship).
The impact of sampling methods on SAR has been empirically tested several times. The results suggest that the SARs rising from the nested design exhibit higher slopes and better fit than independent design based SAR (Drakare *et al.* 2006; Ulrich & Buszko 2007).

2.4. Factors affecting SAR's slope

As far as the slope of the SAR refers to the rate of species accumulation with increasing area, it is crucial to recognize the processes and factors that are responsible for the variability of the reported slopes. As I have already mentioned, all factors that affect species distribution in space, aggregation of species in particular, have distinct impact on the slope of the SAR. In general, factors such as latitude, mean body mass or trophic position are the most commonly described as explaining some variability in the slope of SAR.

i. *Latitude* is one of the traditionally mentioned factors that influence SAR. Slope of SAR is strongly correlated with latitude – with increasing latitude exponent *z* decreases (Drakare *et al.* 2006; Qian *et al.* 2007). This statement is in agreement with decline in β-diversity with increasing latitude (Qian & Ricklefs 2007). This pattern has been observed across all mammalian taxa except bats (Rodriguez & Arita 2004). Some studies did not find expected latitudinal pattern in this group of volant mammals. A probable explanation of this exception consists in flying ability of these mammals. Therefore it is possible that for detection of latitude pattern in bats much larger area range would be needed compared to nonvolant organisms.
ii. *Body mass* also affects species spatial distribution and consequently also exponent *z*. Small organisms (unicellular eukaryotes) exhibit lower values of *z* that is usually explained by their high dispersal ability (Hillebrand *et al.* 2001), which leads to more homogenous distribution in space.
iii. Relationship between the slope of SAR and *mainland* or *island* character of sampled area has been relatively intensively studied in previous decades (Preston 1962b; Rosenzweig 1995). We can apply this basic distinction to any localities that differ in their connectivity to the surrounding areas (e.g. ocean and lakes). According to Rosenzweig (1995) more isolated areas (islands) show steeper SARs compared to mainland areas based on nested design scheme. Drakare *et al.* (2006) pointed out a

negligible difference in *z* between isolated non-contiguous and less isolated contiguous areas by comparing lakes and ocean. Lakes exhibits similar or even lower *z* than ocean areas (depending on design of sampling).

iv. *Trophic rank* also correlates with *z* (Holt *et al.* 1999; Cagnolo *et al.* 2009). Taxa that are located at the bottom of food chain (e.g. plants, gastropods) achieve lower *z* values in comparison with higher positioned taxa (e.g. spiders, birds or even parasitoids). Classical explanation suggests that population size decreases as we move up along the food chain (purely energetic reasons), therefore high trophic rank species are more vulnerable to extinction at small sites and that leads to steeper SAR. Another possible explanation considers *sampling effect*. Once again Drakare *et al.* (2006) did not confirm this relationship between trophic rank and *z*.

v. *Productivity* (quantified as a biomass) negatively correlates with exponent *z* (Wright 1983; Currie 1991; Chiarucci *et al.* 2006). That means that the rate of species richness increase is "slower"in more productive environment. Another evidence promoting this linkage could be found in a study where availability of energy is expressed with NDVI (Normalized Difference Vegetation Index) that is strongly correlated with net primary productivity of environment (Storch *et al.* 2005).

Some other factors affect the slope of SAR. For example forested areas produce higher *z* than non-forested areas (Drakare *et al.* 2006). Drakare did not find any conclusive differences between *z* coming from aquatic and terrestrial realms in his meta-analysis (Drakare *et al.* 2006). Also the intensity of grazing affects the slope of SAR, however, its effect is influenced by climatic conditions and it is not easily interpreted (De Bello *et al.* 2007).

Besides particular factors that impact SAR's slope there has been also several attempts to explain *z* variability theoretically. Recently there has been an increase in the number of macroecologically based papers concerning the SAR. My work is following theoretical principles connecting the slope of the SAR with mean species abundance. Several papers have been focusing on that topic (Harte *et al.* 2009; Šizling *et al.* 2011; Harte *et al.* 2013; Šizling *et al.* 2013) and my aim is to evaluate these considerations with the widest possible dataset gained from literature. The theory predicts that we can explain the majority of SAR´s slope variation using mean species abundances.

To enlighten the basic idea of mean species abundance impact on SAR I will use several parameters I listed above and describe possible connections between them and species abundance. For example body mass has a distinctive effect on abundances. It is obvious that

larger organisms tend to have smaller abundances. The shift from small to big organisms corresponds to the shift from high abundances to low abundances. The effect of increasing body mass is therefore comparable with the effect of decreasing abundance; both of them lead towards steeper slope of SAR curve.

Analogically we can continue with the effect of trophic rank. Higher trophic rank is usually possessed by larger animals that are less abundant in general. Another step of this consideration is the linkage between abundance and the distribution in space. As less abundant species are more sparsely distributed in space we might expect that SAR curve based on these species exhibits steeper slope. On the contrary, species occupying bottom of the food chain are usually smaller (lower mean body mass) and are common (high species abundance). These species are usually widely distributed across the space and when we construct SAR curve with the data about these species we get shallow slopes in comparison to the case described above.

2.5. Abundance and SAR

Evidence of the outlined relationship can be found in the literature. For example, there is a correlation between abundance of butterflies and moths and the slope of SAR (Franzen *et al.* 2012). This study was performed on data from islands located in Baltic and North Sea. The authors took the abundance as a number of individuals recorded per year. There is conclusively steeper SAR belonging to low abundance in comparison with high abundance assemblages. This study presents also correspondence analysis (CA) results that show relatively close links among abundance, body size and diet generalism/specialism (fig 2). Correspondence analysis determines the direction along which the data vary the most (Greenacre & Hastie 1987) and we can call this direction the *principal axis*. As we can see in the figure 2, abundance change (from low abundance toward high abundance level) follows direction given by principal axis that refers to its impact on species assemblages (principal axis represents the most influential variable in the data although the variable might be linear combination of multiple variables, empirically measured variables that follow this direction are therefore the most influential ones). This picture just illustrates the basic idea that abundance could be used as a rough approximation for body size spectrum, degree of diet specialization, etc. in our analyses.

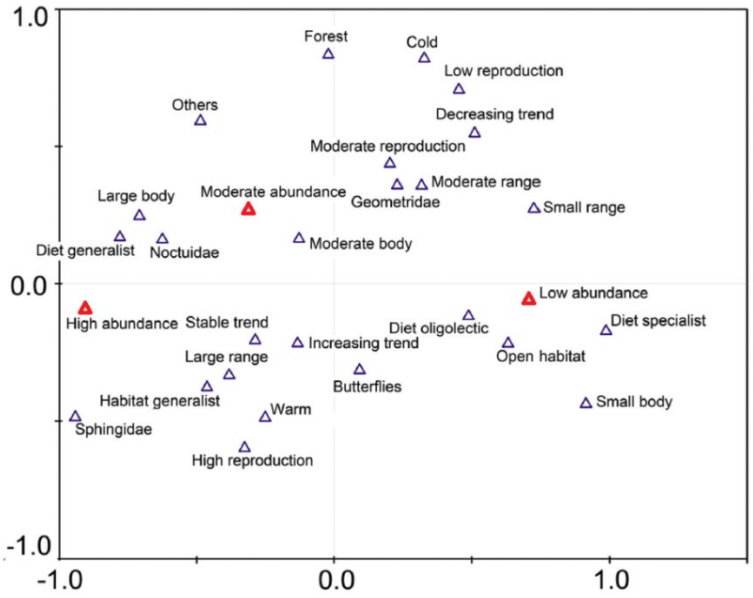

Figure 2: Correspondence analysis showing mutual relations among diverse factors. Abundance levels are highlighted with red triangles (Franzen *et al.* 2012).

There are several theoretical works which show that abundance should affect the slope of the SAR. Harte *et al.* (2009) used maximum entropy (MaxEnt) principle to predict the shape of SAR. This prediction should be widely applicable across all assemblages of different taxonomical affiliation or location as the authors set just few constraints that should present loose analogy to state variables in physics: ecosystem area, total species richness, total number of individuals and total metabolic rate. These constraints somehow define assemblages that could be tested. We may discuss how strong these conditions are and how they narrow the set of possible assemblages (Šizling *et al.* 2011). Harte *et al.* (2009) stated that there is just one universal SAR that is governed by a single predictor, average abundance per species at focal scale *N(A)/S(A)*. This theory is based on several assumptions. Basic assumption is that the sampling design needs to be nested (focal plots are placed within the larger plots). As *N/S* values increases with area (because number of individuals has to increase with area more rapidly than the number of species) predicted values of *z* decrease with area (fig. 3).

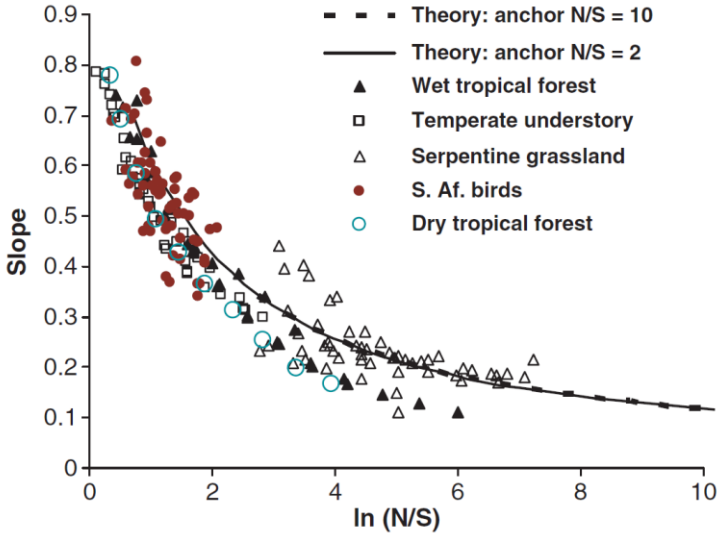

Figure 3: Predicted and observed *z* values dependent on ln (*N/S*). Solid and dashed lines correspond to different anchor values as listed in the figure (Harte *et al.* 2009) (Meaning of anchor values is described in detail in following chapter (Methods))

This article initiated a discussion about the predictive power of that approach. Šizling *et al.*(2011) have shown that the dependence of SAR's slope on *N/S* cannot be universal across taxa. They came with geometrical constraints that determine *z* on the basis of *N/S* but leave some variability that carries biological information. The theory is based on a simple idea. While working with nested design, number of individuals increases with area linearly, this relationship is described as IAR (effect of possible aggregation of individuals is treated by the nested design). SAR has to be placed bellow IAR as there cannot be more species than individuals (see figure 4). SAR also cannot be linear as it has to have lower slope than the IAR (species richness cannot increases linearly, that would be possible only if every sampled individual represents a new species). Therefore SAR curve cannot intersect IAR line and has to bend down. As we can see in the figure 4, the distance (D) between IAR and SAR is enlarging with increasing area. Figure 4 depicted the relationships between number of individuals (N) and number of species (S) on the first axis and area on the second in log-log space. The distance D is log(*N*)-log(*S*), which is $\log\left(\frac{N}{S}\right)$. It suggested that the slope of SAR really could be determined by mean species abundance.

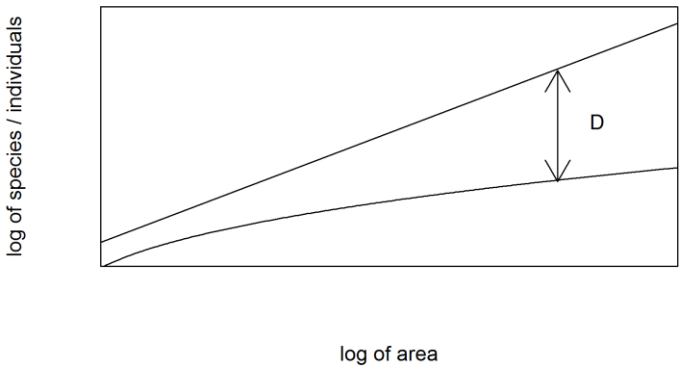

Figure 4: Individuals-area relationship and species-area relationship in a log-log plot. *D* denotes the distance between IAR (upper line) and SAR (bottom curve) that is equivalent to $\log(N) - \log(S) = \log\left(\frac{N}{S}\right)$ (after Šizling *et. al* 2011).

3. Methods

3.1. Data

My aim was to go through the literature and gather all available data concerning the SAR which allow determining its relationship to abundances. The major guideline for me was the review by Drakare *et al.* (Drakare *et al.* 2006) that included the list of studies containing species-area curves (for more details see Table S1 in supporting material for Drakare *et al.*). Besides the slopes of SARs, this list includes also other characterization of the environment and organisms studied. I used this table as a leading line and searched for the studies from the table which were described as based on the nested design. Since Drakare *et al.* gathered studies only until the end of the year 2003, I continued in searching for suitable studies on my own. For that purpose I used Web of Knowledge (topics: species-area relationship, species-area curve, date range: 1.1.2004 – 14.3.2013) and I checked all eligible studies. As I did not constrain the topics directly (I did not use quotation marks) the range of studies I went through encompassed a lot of works mentioning species and area in their abstracts. I also looked for studies with the help of Google and Google scholar.

On account of theoretical prediction I needed to carefully choose the studies for my analysis. I set several conditions I needed to follow. The principal one is the nested design of parcelling the area. There was a lack of these studies, so I also included some studies that did not hold complete nested design. There is a possible alternative to it when smaller plots do not have to be located within larger plot. These plots necessarily have to be found in spatially contiguous area, where dispersal and other biological processes such as lateral growth are enabled (Dengler 2008).

Every species-area curve was provided with several characteristics of the study system. As you can see in the attached appendices while studying overall slopes I operated with following labels: realm, organism, mean body mass, repetition, latitude midpoint, area range, minimal area, maximum area and mean area. Most of these variables were used also in the study I took as guidance (Drakare *et al.* 2006) and we expected that these variables have distinctive impact on slope of SAR curve.

Detailed description follows:

- Realm – This characteristic simply distinguishes between aquatic and terrestrial environment. I treated this variable as categorical. There are two levels of this

variable: “aquatic” and “terrestrial”. Abbreviation in R analysis: *realm*, levels: *realmaqu* and *realmter*.

- Organism – It refers to organism affiliation. There are several levels of this factor such as “birds”, “fishes”, “fungi”, ”helminths”, “plants” and “zoobenthos”. I treated this variable as categorical. Abbrevitation: *org*, levels: *orgbirds*, *orgfishes*, *orgfungi*, *orghelminths*, *orgplants* and *orgzoobenthos*.
- Mean body mass – mean body mass for the group of interest in grams. I used the values stated by Drakare (Drakare *et al.* 2006). In the analysis I operated with natural logarithm of mean body mass to provide more even distribution. Abbreviation: *lnbodymass*.
- Repetition – This factor refers to data achievement. If data were achieved by a single measurement, then repetition equals to 0. In the opposite situation when several measurements lead to averaged values, repetition equals to 1. I came with this characteristic for differentiation of the data that are based on multiple measurement so that I can test whether they fit the MaxEnt predictions (Harte *et al.* 2009) better than the data based just on one measurement. I treated this variable as categorical. Abbrevitation: *rep*.
- Latitude midpoint – Latitude midpoint represents approximate latitudinal middle point of studied area. As I wanted to test the absolute effect of latitude I did not distinguish between Southern and Northern Hemisphere and I operated with absolute values. Furthermore, the total majority of gathered data originates from Northern Hemisphere, and thus comparison between hemispheres would not be possible due to unbalanced design. Abbrevitation: *latmid*.
- Area range – it is defined as $\ln(A_{max}/A_{min})$, A_{max} marks the largest sampled site, A_{min} marks the smallest sampled site. Abbreviation: *arange*.
- Mean area – mean value of all sites sampled for the construction of single species-area curve. The purpose of this characterization consists in determining the position on the species-area curve (having in mind triphasic character of this curve). In the analyses I operated with logarithmically transformed mean area. Abbreviation: *lnmeana*.

While analysing local slopes I operated with several more labels assigned to each value of the slope:

- Focal area – size of the area that is attributable to local slope. In my case, when I computed local slope from two areas (A_n and A_{n+1}) I assigned smaller plot (A_n) to

computed slope value. In the analyses I operated with logarithmically transformed focal area. Abbreviation: *lnarea*

- Plot – this categorical variable describes the situation that several local slope values belong to the same SAR curve. Therefore, these values should differ among each other less than in comparison with other local slopes belonging to different SAR curves. Abbreviation: *plot*
- Study – according to the hierarchical structure in data, in some studies several plots were examined and therefore, there is a higher probability that these studies are spatially correlated more (*i.e.* more similar) than plots originating from different studies. Abbreviation: *study*

I have performed two groups of analysis. At first I examined overall slopes of SAR (linear regression in log-log space). Next I explored relationships between local slope of the SAR and other variables (for further comments see Chapter 2.3 Data Analysis).

For the analysis concerning overall slope of the species-area curve I incorporated broader range of studies **(**see apendices). Analyses that operate with local slopes needs stricter attitude. For example I excluded studies that work with non-contiguous plots, non nested designs and studies whose plots were enlarged by ε larger than 10

I needed to get *z* values coupled with the mean species abundances of the assemblages. There were several ways I obtained these data. In some studies I directly found total number of individuals *N* and after dividing it by number of species *S* I got required information (*N/S*). Other studies provided data about mean density or mean biomass. In those cases I just calculated *N* using total area of plot or mean body mass. Several times the papers do not hold any information referring to abundances. Then I was looking for studies focused on the same group of organisms in the same area and ideally in the close time span. Because of the procedures listed above some resulting abundances represent only rough estimates. As long as I am working with logarithms of abundances I assume the accuracy of the abundance data is sufficient enough.

Despite my original aim I was not able to collect as wide dataset as we planned. Majority of SAR studies are based on island data and mostly do not use nested design for the construction of species-area curves. Therefore, this huge portion of SAR studies cannot be included in my analysis. Another difficulty was represented by lack of abundance data especially for some organism groups. That leads to rather unbalanced dataset with regards to the organism position on the “tree of life”, with distinct predominance of vascular plants.

For complete data sets concerning overall and local slopes see Appendix A and Appendix B, respectively.

3.2. Data processing operations

In first part of my work I operated with overall slopes of SARs (species increase with area in log-log space). I directly used the slope value from the papers or (when unavailable) I computed the slope of the regression line. Sometimes neither of nominal values were included in the paper. In that case I used PlotDigitizer software (Huwaldt 2012) to digitize the plot of measured species richness on different areas. This approach might not be perfectly precise, but it was the only way how to access the data and the accuracy was sufficient for my analysis.

While working with the local slopes of the SARs I needed to define and compute several coeficients. I will describe my steps in more detail in following lines.

At first, proportion between two following areas, ε (epsilon) is computed:

$$\varepsilon = \frac{A_{n+1}}{A_n}.$$

A stands for area, lower indices specify the relationship between sites where *n is* the initial stage (smaller area) and *n+1* is the next stage (larger area).

With the help of ε we may compute local slope of the species-area curve. Z_{loc} calculation corresponds to the derivation calculation. The difference is in the size of epsilon. Then

$$z_{loc} = \frac{\ln(S_{n+1}) - \ln(S_n)}{\ln \varepsilon},$$

where *S* stands for the number of species, and lower indices keep their meaning.

Further analyses were based on the thoughts of Šizling *et al.* (Šizling *et al.* 2011). In equation 9 they state

$$z \cong 1 - \frac{\ln(1+J_\varepsilon)}{\ln \varepsilon},$$

where *J* is Jaccard index referring to the percentage of species shared by two assemblages (Jaccard 1901). This relation is valid only for $\varepsilon = 2$. In my dataset epsilon could differ from two, so I needed to modify Jaccard index. That is why I performed some corrections that are described properly in following lines. These adjustments allowed me to operate with data coming from different studies (differing in ε) and compare them with each other. First, we need to express the equation in the form

$$J_\varepsilon = e^{(1-z)\cdot\ln(\varepsilon)} - 1.$$

Since *z* has to be an element of [0, 1], we need to look at the marginal cases.

If $z = 0$, then $J_\varepsilon = \varepsilon - 1$.

If $z = 1$, then $J_\varepsilon = 0$.

In general, *J* is meaningful between 0 and 1 (including also 0 and 1) and our maximum value is $\varepsilon - 1$, so we need to rescale *J*. With following procedure we get J_n that is an element of [0, 1] and is analogous to J_ε even for epsilon differing from two:

$$J_n = \frac{J_\varepsilon}{\varepsilon - 1}.$$

Another equation from Šizling *et al.* (Šizling *et al.* 2011) that is crucial for my analysis is equation 7, that states

$$J_{n+1} \cong \frac{K \cdot J_n}{2 - K \cdot J_n}.$$

We need to express the equation in another form once again, so that we get

$$K = \frac{2 \cdot J_{n+1}}{J_n \cdot (1 + J_{n+1})},$$

K thus refers to the J_{n+1} value and as input it uses only J_n value. We might say that *K* determines the value of z_{n+1}.

For each particular local slope in each study I computed the coefficients mentioned above.

I also operated with parameter K (based on the percentage of shared species on plots on the same spatial scale) that denotes the behaviour of *z* on the following spatial scale (whether *z* decreases or increases). Higher *K* leads to a stronger decrease in *z* between focal and consecutive scale. There are specific limitations based upon this parameter. With respect to its technical character, I placed these considerations into following box (Box 1).

Box 1: K parameter

K is constrained by 1 from below and by smaller value of 4 and $\frac{1}{J_n}$ from above that is a result of theoretical considerations. Basic idea of these constraints could be illustrated by the figure number 5. Fig. 5 represents set of fine grid cells (A1, A2, B1, B2) that merge into coarser scale grid cells (A, B). This setting is equivalent to $\varepsilon = 2$ as coarser scale area is double size of finer scale area. We might claim that Jaccard index (the proportion of species shared by the two assemblages from the total number of species) between two adjacent plots of a given area (J_n) constrains Jaccard index between two adjacent plots of twice that area (J_{n+1}). This influence of J_n could be described by this equation: $J_{n+1} \cong \frac{KJ_n}{2-KJ_n}$, where the parameter K is constrained as $1 \leq K \leq \min\left[4, \frac{1}{J_n}\right]$. I will clarify reasons leading to these constraints according to Šizling *et al.* (2011):

i. Jaccard index is defined as a proportion of species shared by two plots.

ii. The number of species shared by two adjacent larger plots (A, B) cannot be lower than the mean number of species shared by two finer subplots – each affiliating to different larger plot (i.e. mean number of species between A1 and B1, A1 and B2, A2 and B1, A2 and B2).

iii. The number of species shared by two adjacent larger plots (A, B) cannot be more than four times higher than this mean number of shared species (defined in previous lines)

iv. K cannot exceed the value of $\frac{1}{J_n}$ as Jaccard index can never exceed 1 (more precisely described in Appendix B, Šizling *et al.* (2011))

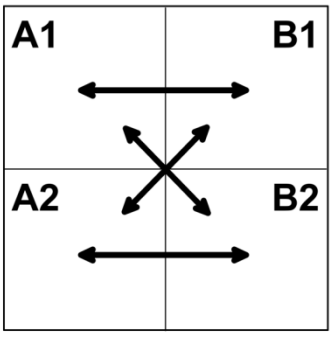

Figure 5: Spatial grid cells at finer (A1, A2, B1, B2) and coarser scale (A, B) according to Šizling *et al.* (2011)

K parameter allows us to determine *z* value at the next coarser scale once we know *z* at the focal scale. It might be valuable while trying to determine the shape of SAR on coarser scales from empirical values for finer spatial areas.
Recent discussion of Harte *et al.* (Harte *et al.* 2013) and Šizling *et al.* (Šizling *et al.* 2013) about the universality of MaxEnt-based theory of ecology suggests that this area of macroecology is rapidly changing and there is a need of empirical confirmations or refutations of the theoretical principles.

3.3. Data analysis

All the analysis were performed in R (R Development Core Team 2008), using RStudio, an integrated development environment for R (RStudio Inc. 2012). I usually rounded the numbers to three decimal places. I was looking for advice about statistical issues as well as programming ones in several books while working in R environment (Crawley 2007; Pekár & Brabec 2009, 2012). There are several notes in following chapters that refer to R functions or scripts; I used Courier New font for these words to highlight them in the text.

At first I needed to decide how to handle predictions by Harte *et al.* (2009). Because of the complexity of this theoretical MaxEnt based concept at the very beginning I digitized figure 1a (figure 3 in my work) from above mentioned article with the help of PlotDigitizer (Huwaldt 2012). Therefore, I obtained predicted values for the slopes of SAR curves together with particular values of logarithm of mean species abundance, ln(N/S). To provide better handling of this prediction while fitting various models I approximated these values by the function that suits the data best (compared by the coefficient of determination, R^2). Therefore there is no need to look for biological meaning of parameters of this function as it just simplifies our work with models. In order to find the function I used TableCurve 2D (Systat Software inc. 2002). This program produces a list of various functions that fit the data and gives several characterizations to all of these functions, their goodness of fit *etc*. I picked up the one with the highest coefficient of determination (R^2=0.999):

$$\frac{1}{z} = 0.873 + 0.753 \cdot \ln\left(\frac{N}{S}\right).$$

In following lines, when Harte *et al.* or MaxEnt prediction are mentioned I have this approximation, that I operated with, in mind.

Apart from digitizing the plot from the paper I already quoted I wanted to verify the method that Harte *et al.* (2009) described. Therefore, I numerically solved the equations that gave me *z* values for different *N/S*. Whole procedure of calculating these values is described in more details in following lines.

At first I needed to set initial values for number of species (S_0) and number of individuals within these species (N_0). I chose one of two anchor values that Harte *et al.* (2009) worked with:

$$S_0 = 100,$$
$$N_0 = 10.$$

The prediction for *z* for several spatial scales was computed, gradually ascending the area. The area in each step was enlarged by coefficient $\varepsilon = 2$. As for beginning, Harte's formula (3) was used. It states:

$$\frac{S_0}{N_0}\sum_{n=1}^{N_0} e^{-\lambda_{\phi,0}n} = \sum_{n=1}^{N_0}\frac{e^{-\lambda_{\phi,0}n}}{n}.$$

S_0 and N_0 values were substituted with anchor values and numerical value for $\lambda_{\phi,0}$, the Lagrange multiplier, was received. Then this value was substituted into Harte's formula 11 and finally I received value for *z*:

$$z(A) \approx \frac{1}{\ln(2)\ln\left(\frac{1}{\lambda_{\phi,A}}\right)}.$$

Now, *z* value for area *A* was known. So it was possible to enlarge area by ε and move to the area 2*A*. Obviously, $N(2A) = 2 \cdot N(A)$ as number of individuals increased proportionally with area, but the value for *S(2A)* was needed. Harte's formula 9 was used:

$$\frac{S(2A)}{N(2A)}\sum_{n=1}^{N(2A)} e^{-\lambda_{\phi,2A}n} = \sum_{n=1}^{N(2A)}\frac{e^{-\lambda_{\phi,2A}n}}{n}.$$

Value for *S(2A)* was received, expressed with $\lambda_{\phi,2A}$. This expression was substituted into Harte's formula 8 in which our last numerically unknown variable is also $\lambda_{\phi,2A}$:

$$S(A) = S(2A)e^{\lambda_{\phi,2A}} - N(2A)\frac{1-e^{-\lambda_{\phi,2A}}}{e^{-\lambda_{\phi,2A}} - e^{-\lambda_{\phi,2A}(N(2A)+1)}}\left(1 - \frac{e^{-\lambda_{\phi,2A}N(2A)}}{N(2A)+1}\right).$$

I got numerical value for $\lambda_{\phi,2A}$ and once again substituted it into equation 11 from Harte *et al.* (2009). Finally I received *z* for area *2A*. In following step I needed to operate with *2A* values as focal scale and *4A* values as coarser scale. I repeated this procedure and upscaled gradually.

Then set of *z* values was received linked with different *N/S* values. Finally I compared these results with digitized values and realized that both approaches led to the same outcomes.

Basically I can divide the analyses I performed into five groups:

i. Exploratory data analysis (EDA)
ii. Analysis concerning overall slopes of SARs (*z*), in which I included also mean species abundance, ln(*N*/*S*), as one of the predictors.
iii. Analysis concerning local slopes of SAR (local *z*), predictor ln(*N/S*) included as well.
iv. Analysis focusing on the residuals of overall slopes after fitting prediction of Harte *et. al* (2009).
v. Inquiry into K parameters and their comparison with the predictions about its distribution (Šizling *et al.* 2011).

Although Harte *et. al* (Harte *et al*. 2009) predictions has been intended and computed for local slopes of SAR curves, I examined also its impact on overall slopes.
As my data set was non-orthogonal I used backward stepwise regression (simplification of a complex model). Furthermore, I was not able to operate with interactions among predictors due to the non-orthogonality (there were no data for some interactions at all). While working with non-orthogonal data I standardized the variables to avoid possible correlations among the explanatory variables.´

i. Exploratory data analysis (EDA)

At first I explored my datasets (overall and local slope values) and I calculated few basic characteristics. I also examined my data with help of graphical means. Afterwards, I used `tree` package in R (Ripley 2013) to visualize possible interactions among the predictors according to the tree models theory (Crawley 2007).

ii. Overall slopes

At the very beginning of my analyses I treated missing values in my data set. As there was just one incomplete data input in my data I removed it. This removed value was the only one that represented the *organism* level *fishes*.

Then I inspected the predictive power of MaxEnt on overall slopes of SAR curves in my data set. I computed coefficient of determination for the prediction.

Afterwards I operated with linear models starting with the maximal model (but containing only main effects due to the lack of data for some interactions). During whole process of analysing I operated with standardized variables (after the scaling and centralizing all the variables, both response and explanatory, have the mean value of zero and variance equals of 1). All the variables that are standardized might be distinguished in the R outputs as they are labelled with the extension ".std". I also standardized quadratic terms of continuous variables (labelled with the extension ".sq.std"). This standardization allowed me to compare the effects of all various variables.

I examined simplification of the model following instructions in The R book (Crawley 2007). I removed the least significant predictors and checked whether the deletion did not cause significant change in deviance. If the change of deviance was significant I did not remove the predictor from the model. I continued by repeating these steps to the minimal adequate model. I have to point out that due to the non-orthogonality of the data the order of explanatory variables in model specification does matter and influence the results. However, if handled properly, even simplification of models based on non-orthogonal variables can be performed without major problems connected with the order of predictors in the input (*e.g.* for validating of variable's significance I used the function `summary()` instead of `anova()`). I also checked the Akaike information criterion (AIC) of the models. If the deletion of the predictor did not cause significant change in deviance (was therefore plausible) but raised AIC, I kept it in the model.

When I reached final model I inspected the impact of each particular predictor with comparison of change in R^2 that is attributable to single predictors.

iii. Local slopes

There were several data points that had ln(N/S) values below ln(2), that is the minimal value predicted by Harte *et al.* (2009). It was caused by the fact that starting values of N/S for calculations were 40/20 and 100/10. Even when I used values $N = 40$ and $S = 20$ I could not come closer to *y* axis than ln(2). That is why I removed these values from the dataset (it was 22 values from the overall number of 436 values).

After these adjustments I wanted to measure the goodness of fit of MaxEnt predictions. Therefore, I computed the R^2 value.

Afterwards, I moved on to the analysis of the best linear combinations of predictors for explaining the variability of local slope values. I operated with the whole data set, no values were excluded. Once again I operated with standardized variables (both response and explanatory variables). I needed to respect the arrangement of my data as several local slopes belonged to one particular SAR curve and suggested the dependency among the values. This structure in my data required using linear mixed models. While operating with these models I followed the advice and procedures from several books (Crawley 2007; Zuur *et al.* 2009; Pekár & Brabec 2012); mainly Zuur *et al.* (2009) described the whole procedure of handling linear mixed effects models, so I stuck to their recommendation. To facilitate the dealing with models I used `nlme` package in R (Pinheiro *et al.* 2012). I started with a model containing all explanatory variables and the quadratic terms of continuous variables as fixed components. I did not include interactions because of unbalanced data set. According to Zuur *et al.* (2009) this model is called *beyond optimal* model. After defining this model I needed to find the best arrangement of random effects. When random effects are solved and the appropriate one is picked up and used in the model, there is time to optimize the structure of fixed effects. This way should bring us to the optimal, final model.

iv. Residuals of overall slopes after fitting the prediction

I was interested in finding the linear combination of predictors that would explain some variability of residuals after fitting the MaxEnt prediction. I also operated with standardized variables as I mentioned before. Then I updated the model by removing the least significant explanatory variable. If the removal did not significantly change the deviance I kept the variable in the model and repeated the process of removing variables in the same way until I found the minimal adequate model.

v. *K* parameter

With respect to the nature of predictions towards the distribution of *K* values (Box 1) I decided not to perform any rigorous analysis. Therefore only the depiction of empirical values and their constraints follows in the following chapter. I still needed to decide how to handle the $\frac{1}{J_n}$ constraint as I wanted to draw this constraint as a simple line and the $\frac{1}{J_n}$ led to the set of values that did not form any strict curve. Therefore, I calculated $\frac{1}{J_n}$ values for each particular z value from the data and used TableCurve 2D (Systat Software inc. 2002) to find the suitable

fit. I picked up following function from the list of fitting functions: $\frac{1}{J_n} = 1.095 - \frac{1.604 \cdot local\ z}{\ln(local\ z)}$, whose fit to the data was satisfying (R^2=0.928). After this procedure I was able to examine the distribution of *z* values with respect to predicted constraints.

4. Results

i. Exploratory data analysis

Several basic statistical characteristics were calculated for two basic data sets. Obtained values are listed in table 1.

Table 1 Main descriptive statistical characteristics of my data sets

	Overall slope	**Local slope**
Mean	0.363	0.299
Median	0.350	0.290
Range	$[0.050, 0.850]$	$[0.003, 0.811]$
Confidence interval	$(0.323; 0.403)$	$(0.284; 0.315)$
Variance	0.032	0.027

Except for some descriptive labels I also included simple histograms illustrating the distribution of overall and local slopes.

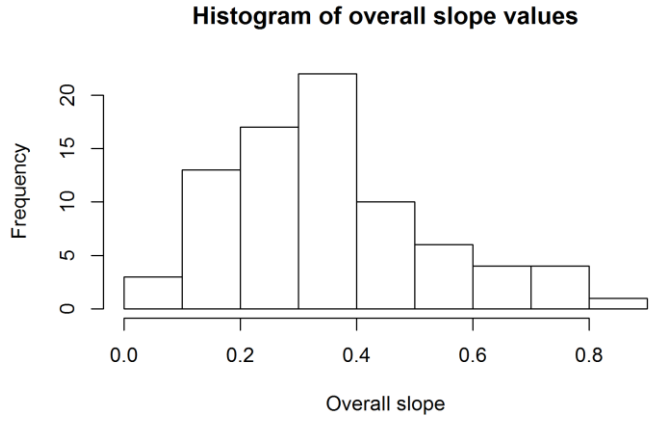

Figure 6 Comparison between the histograms for overall and local slope values.

Tree models are usually used as a guideline when there are many explanatory variables and we would like to have some brief insight into the data to realize what variables are the most influential. As for the overall data I restricted the structure of the model to 6 nodes (this decision was made after examining the relationship between total deviance and complexity of model, where 6 nodes seemed to represent a meaningful compromise). For graphical representation of tree model for overall slopes, see figure 7.

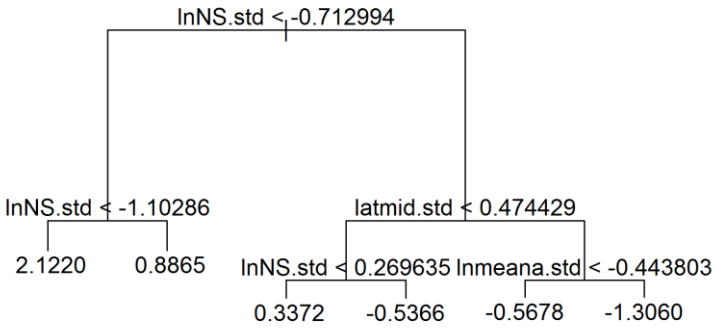

Figure 7 Visualization of tree model for overall slopes, all variables used in the model are standardized (scaled and centralized).

As we can see in figure 7, the most important explanatory variable from all I included (*realm*, *organism*, *latitude midpoint*, *area range*, logarithm of *mean species abundance*, logarithm of *mean area*, logarithm of *mean body mass*) is *mean species abundance*. For lower *mean species abundance* values, there is a significant impact of *mean species abundance* that brings some more detailed distinction. For values of standardized logarithm of mean species abundance higher than -0.713, there is a considerable role of *latitude midpoint*. Important threshold is presented by standardized value of *latitude midpoint* 0.474. Areas lying closer to the equator are consequently influenced by *mean species abundance*, whereas areas that are more remote from equator are more impacted by logarithm of *mean area.*

There was a little bit more complicated situation when I operated with local slope values. As tree modelling is able to operate only with factors (categorical variables) with limited amount of levels I was forced to omit *study plot* and *study* affiliation from the model. Therefore, the

hierarchical structure cannot be seen in the model (by hierarchical structure I mean that several local slopes are binded through one *study plot* and sometimes few *study plots* belong to the same study). Once again I decided to set up the complexity of the model to 6 nodes. For the results of tree model for local slopes see figure 8.

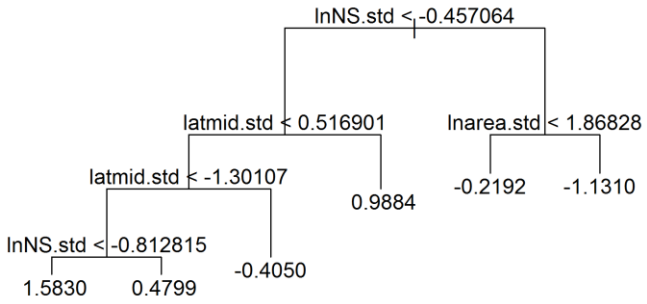

Figure 8 Graphical representation of tree model for local slopes, all variables in the model are standardized.

Figure 8 suggests high influence of *mean species abundance* on local slopes (but remember ommiting of the hierarchical structure), that is followed by important impact of *focal area* for higher values of *mean species abundance.* On the other hand, for lower values of *mean species abundance*, there is a distinctive effect of *latitude midpoint.*

Overall slopes

I examined the ability of Harte *et al.* (2009) prediction to explain the variability of overall slopes of SAR curves by computing the coefficient of determination. I received R^2 equal to 0.540. The goodness of fit is illustrated in the figure number 9.

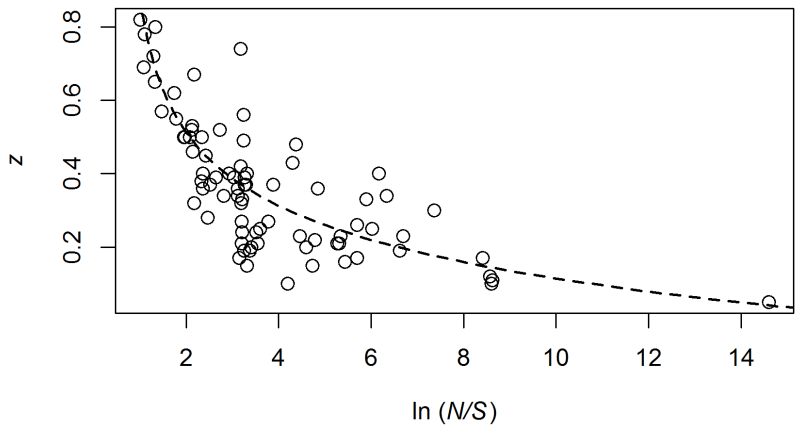

Figure 9 Illustration of overall slopes obtained from the literature (open circles) and MaxEnt based prediction (Harte *et al.* 2009) (dashed line).

Then I examined which explanatory variables are the best predictors for overall slopes of SAR curves. The maximal model encompassed following explanatory variables: *realm*, *mean body mass*, *latitude midpoint*, *area range*, logarithmically transformed *mean area*, *organism* and logarithmically transformed *mean species abundance*. All of these variables were standardized as I mentioned.

After the inspection of final model that came out of linear combination of these predictors (mainly the plot of residuals vs. fitted values) I added also quadratic terms of continuous variables. I modified the structure of *organism* variable to reduce the complexity of model. I merged several levels together (levels merged: helminths, plants, zoobenthos; new variable: *org2*) as it did not cause any significant change in deviance of the model. Final validation of models revealed that few data points had immense impact on the model. Cook's distances of these data points were >1 in one case and >0.5 in the second case. I decided to remove these data points from the data set and after these adjustments I started with model simplification once again from the beginning. Final model validation also revealed that there were several data points that had large leverage value. That was caused by unbalanced data as, for example; some levels of *organism* variable were represented by just few values (birds), sometimes even by only one value (fungi).

During the simplification of the model quadratic term of logarithm of *mean body mass*, *area range, realm* and logarithm of *mean area* were removed.

I enclosed also commented R script to clarify the procedure I performed:

At first I defined the maximal model:

```
lm2<-
lm(z.std~arange.std+lnmeana.std+lnbmass.std+lnNS.std+realm+org2+latm
id.std+lnNS.sq.std+latmid.sq.std+arrange.sq.std+lnmeana.sq.std+lnbma
ss.sq.std, data=adjdata)
```

I inspected the model and checked the correlations between explanatory variables:

```
summary(lm2, corr=T)
```

I started with removing the least significant predictors:

```
lm3<-update(lm2,~.-lnbmass.sq.std)
```

Then I checked the impact of the deletion and continued with another deletion of unsignificant predictors all the way to the minimal adequate model:

```
anova(lm2,lm3)
summary(lm3)
lm4<-update(lm3,~.-realm)
anova(lm3,lm4)
summary(lm4)
lm5<-update(lm4,~.-latmid.sq.std)
anova(lm4,lm5)
summary(lm5)
```

I also validated the model through the graphical means:

```
plot(lm5)
```

I checked the AIC values as I needed AIC to decrease in each step:

```
AIC(lm1, lm2, lm3, lm4, lm5)
```

Finally I extracted R^2 value from the model summary:

```
summary(lm)[[8]]
```

This model explains 83% of variability of overall slopes (R^2=0.834). The most significant predictors (measured by *p*-values) are *mean species abundance*, quadratic term of *mean species abundance* (that suggests that the effect of *mean species abundance* is nonlinear) and *organism* (level "fungi").

Summary of the final model follows immediately as I found this R output more clearly arranged than simple description of results in the text. The abbreviations used in R hopefully intuitively refer to the predictors (described in chapter 2.1 with appended abbreviations). In few first lines of R output, distribution of residuals is described with help of minimal and maximal values, first and third quadrats and median. Values I received confirmed basic assumptions imposed on distribution of residuals (symmetrical distribution with median close to 0). In the first column of the table the estimates of parameters or effects are listed (`Estimate`). Standard errors of estimate (`Std. Error`), t values `(t value)` and p values `(Pr(>|t|))` follow in the other columns. I operated with treatment contrasts in which the impact of changes in variables (both categorical and continuous) is compared with referring combination of variables. In R analysis that I performed, levels of categorical variables were lined up according to the alphabetical order. First (reffering level) was then represented by *bird* in *organism*. We have to keep in mind that estimates for unique levels enlisted in table reflect differences from the referring level. Little complicated situation was detected with levels of *organism*. I merged several levels of *organism* into one (helminths, plants and zoobenthos) so in the analysis just 3 levels could be distinguished (birds, fungi, helm.plant.zoobent). We have to take into account that *plant* level is the only one that is well represented in the data. As standard errors of estimates indicate, other levels are based on few data that led to wide ranges of estimated parameters.

```
Call:
lm(formula = z.std ~ arange.std + lnmeana.std + lnbmass.std +
    lnNS.std + org2 + latmid.std + lnNS.sq.std + arange.sq.std +
    lnmeana.sq.std, data = adjdata)

Residuals:
```

```
     Min       1Q   Median       3Q      Max
-0.85184 -0.27550 -0.03254  0.27763  0.87105

Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)              -1.4420     0.8024  -1.797 0.076822 .
arange.std                0.8588     0.2936   2.925 0.004695 **
lnmeana.std               0.8305     0.3069   2.706 0.008619 **
lnbmass.std              -0.2335     0.1170  -1.995 0.050096 .
lnNS.std                 -2.8055     0.4506  -6.227 3.57e-08 ***
org2fungi                 4.0691     0.9911   4.106 0.000112 ***
org2helm.plant.zoobent    1.6163     0.8514   1.898 0.061969 .
latmid.std               -0.2098     0.1448  -1.449 0.152080
lnNS.sq.std               3.2544     0.6779   4.801 9.22e-06 ***
arange.sq.std            -0.7596     0.3112  -2.441 0.017311 *
lnmeana.sq.std           -0.6437     0.3508  -1.835 0.070931 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.4298 on 67 degrees of freedom
Multiple R-squared: 0.8343,     Adjusted R-squared: 0.8096
F-statistic: 33.74 on 10 and 67 DF,  p-value: < 2.2e-16
```

I also admitted the possibility that slopes for the SAR curves that were gained from the same paper might be correlated (some plots that were studied in one study were close to each other). That is why I constructed also linear mixed effects model with random intercept effect (intercepts differ among singular studies), which allows operating with values belonging to similar environment or conditions and might be correlated due to this fact. I compared this linear model with linear model by the means of AIC and I rejected the idea of using linear mixed models for the purposes of analyzing the overall slopes variability as AIC value for model with random intercept effect was higher than AIC belonging to simple linear model (I followed instructions by Zuur *et al.* (2009), page 121).

As I wanted to inspect the impact of each predictor in final model on response variable I compared the change in R^2 that indicate the amount of variability in slope values attributable to each single predictor. My procedure consisted in comparing R^2 (explained variability) of full model that included all the predictors with R^2 of the model where one predictor was

removed (R^2 of full model minus R^2 of adjusted model). This way I obtained the amount of variability in response variable that is attributable only to this particular predictor. By this procedure I obtained the results that are listed in table 2.

Table 2 Changes in R^2 (ΔR^2) that are attributable to single explanatory variables; quadratic terms of variables are marked with upper indices.

Explanatory variable	**ΔR^2**
Logarithm of mean species abundance	0.096
Organism	0.076
(Logarithm of mean species abundance)^2	0.057
Area range	0.021
Logarithm of mean area	0.018
(Area range)^2	0.015
Logarithm of mean body mass	0.010
(Logarithm of mean area)^2	0.008
Latitude midpoint	0.005

I used the change in R^2 to set the most influential variables. According to that idea I prepared another table that summarizes the effects of most powerful predictors (table 3).

Table 3 Most influential predictors for overall slope values and estimates of standardized regression coefficients (β coefficients); *organism* turned out to be the most influential predictor but as it is a factor with several levels, its effect is more complicated.

Explanatory variable	**β coefficient**
Organism	Factor
Logarithm of mean species abundance	-2.805
(Logarithm of mean species abundance)^2	3.254
Area range	0.859

ii. Local slopes

First, my aim was to set the predictive power of MaxEnt approach. I calculated R^2 for Harte *et al.* (2009) prediction. I received $R^2 = 0.0093$, that indicates poor quality of prediction.

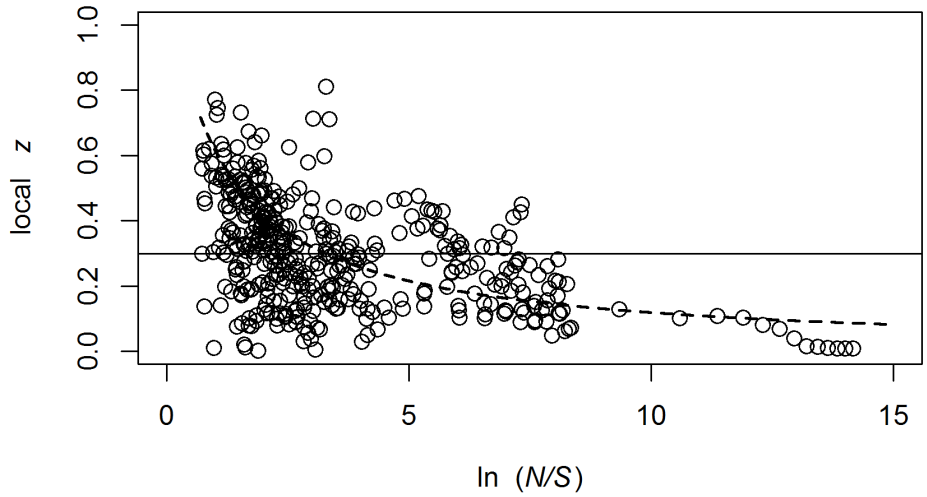

Figure 8 Illustration of local slopes obtained from the literature (open circles) and MaxEnt based prediction (Harte *et al.* 2009) (dashed line); solid line represents the mean value for local slopes.

Afterwards I wanted to find the best model to predict *local slope* values with the help of all other predictors (*mean species abundance* included).

Once again I enclosed commented R script (`locz` stands for *local slope* in the script):

At the very beginning I defined three models differing in the random part. The first one (`gls1`) did not contain any random effects; the second model (`lmeslope1`) was specified with random component that allowed the intercept to differ among different study plots (`plot`). The third model encompassed even more complicated random component where study plot was nested within a study (`stud/plot`). Note that I used REML (restricted maximum likelihood estimation) to specify the models:

```
gls1<-
gls(locz.std~1+lnNS.std+realm+org+lnbmass.std+latmid.std+lnarea.std+
lnbmass.sq.std+latmid.sq.std+lnarea.sq.std,data=locsloper,
method="REML")
lmeslope1<-
lme(locz.std~1+lnNS.std+realm+org+lnbmass.std+latmid.std+lnarea.std+
lnbmass.sq.std+latmid.sq.std+lnarea.sq.std,random=~1|plot,
data=locsloper, method="REML")
```

```
lmeslope2<-
lme(locz.std~1+lnNS.std+realm+org+lnbmass.std+latmid.std+lnarea.std+
lnbmass.sq.std+latmid.sq.std+lnarea.sq.std,random=~1|stud/plot,
data=locsloper, method="REML")
```

I compared all the models using AIC to pick up the best random component. While comparing the models that differ in random components it is necessary to operate with REML instead of ML (maximum likelihood). The lowest AIC value was obtained in the model with the most complex random component (`lmeslope2`), therefore I used that one as a maximal model for further analyses:

```
AIC(gls1,lmeslope1,lmeslope2)
```

For comparison of models differing in fixed effects we must use ML estimators. After this adjustment I inspected the model with `summary()` function and prepared two models. I removed the first and the second least significant predictors in these models (just one in each of them). Then I performed ANOVA test (analysis of variance) between maximal model and these two adjusted models to test the impact of deletion of a predictor. I preferred the model with smaller impact on deviance for further analyses:

```
ML1.full<-
lme(locz.std~1+lnNS.std+realm+org+lnbmass.std+latmid.std+lnarea.std+
lnbmass.sq.std+latmid.sq.std+lnarea.sq.std,random=~1|stud/plot,
data=locsloper, method="ML")
summary(ML1.full)
ML1.A<-update(ML1.full,~.-lnNS.std)
ML1.B<-update(ML1.full,~.-realm)
anova(ML1.full, ML1.A)
anova(ML1.full, ML1.B)
```

I repeated this procedure until I reached the minimal adequate model. I stopped removing the predictors when AIC value started to increase:

```
summary(ML1.B)
ML2.A<-update(ML1.B,~.-lnNS.std)
```

```
ML2.B<-update(ML1.B,~.-lnarea.sq.std)
anova(ML1.B, ML2.A)
anova(ML1.B, ML2.B)
summary(ML2.B)
ML3.A<-update(ML2.B,~.-lnNS.std)
anova(ML2.A, ML3.A)
summary(ML3.A)

AIC(ML1.full, ML1.B, ML2.B, ML3.A)
```

I inspected the quality of final model with the plot of residuals vs. fitted values:

```
E2<-resid(ML3.A, type="normalized")
F2<-fitted(ML3.A)
plot(x=F2, y=E2)
```

As we can see in the script above the *beyond optimal* model encompasses these predictors: logarithm of *mean species abundance*, *realm*, *organism*, logarithm of *mean body mass*, *latitude midpoint*, logarithm of *focal area* (abbreviation *lnarea*) and quadratic terms of all continuous variables (except from the *mean species abundance*). Structure of random components is described above. During the simplification of the model I removed *realm*, quadratic term of logarithmically transformed *focal area*, logarithm of *mean species abundance*. Finally at the end of the process of model selection, these predictors were among the most significant ones: logarithm of *mean body mass*, quadratic term of *latitude midpoint* and logarithm of *focal area.*

Another analysis that could be performed is the variance components analysis that distinguishes the portion of variance attributable to partial levels in hierarchical structure. I operated with standard deviations attributed to different hierarchical levels and computed the portion of overall variance in the model that is connected to these levels. This way I find out that the most important component of overall variance is the variance among the particular values of local slopes (58.044%). The second most important is variation from one *study plot* to the others (41.955%). The rest of variance belongs to the variance among the *studies*, that means that really small portion of overall variance (<< 1%) could be accounted to the differences among particular papers.

```
Linear mixed-effects model fit by maximum likelihood
 Data: locsloper
       AIC      BIC    logLik
  961.0334 1005.888 -469.5167

Random effects:
 Formula: ~1 | stud
         (Intercept)
StdDev: 5.073883e-05

 Formula: ~1 | plot %in% stud
        (Intercept)  Residual
StdDev:   0.5414965 0.6369167

Fixed effects: locz.std ~ org + lnbmass.std + latmid.std +
lnarea.std + lnbmass.sq.std +      latmid.sq.std
                    Value Std.Error  DF   t-value p-value
(Intercept)     1.1663995 0.5118202 372  2.278924  0.0232
orgplants      -2.1907380 0.5888479   9 -3.720380  0.0048
orgzoobenthos  -0.6123303 0.5167252   9 -1.185021  0.2664
lnbmass.std     0.8649133 0.2168699  47  3.988167  0.0002
latmid.std     -1.8386261 0.4516552  47 -4.070862  0.0002
lnarea.std     -1.0420860 0.1270954 372 -8.199239  0.0000
lnbmass.sq.std -0.4360668 0.1785321  47 -2.442512  0.0184
latmid.sq.std   1.1750697 0.4646333  47  2.529026  0.0149
 Correlation:
               (Intr) orgpln orgzbn lnbms. ltmd.s lnr.st lnbm..
orgplants      -0.925
orgzoobenthos  -0.939  0.803
lnbmass.std     0.014 -0.255  0.126
latmid.std     -0.147  0.113  0.121 -0.215
lnarea.std     -0.418  0.598  0.261 -0.575  0.000
lnbmass.sq.std -0.064  0.230 -0.054 -0.671  0.651  0.233
latmid.sq.std   0.049  0.066 -0.084  0.159 -0.927  0.137 -0.468

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
```

```
-3.53041199 -0.53043037 -0.07417268  0.48941081  4.56822222

Number of Observations: 436
Number of Groups:
          stud plot %in% stud
            12             63
```

As I operated with linear mixed effect models in this part of my work, I could not state the importance of particular variables with help of R^2 coefficient. Therefore I used standardized regression coefficients (β coefficients) for comparing the influence of predictors. In table 4 we can see the predictors and β coefficients attributable to them (predictors ranked from the most influencing one to the least).

Table 4 Comparison of β coefficients of explanatory variables for local slope values.

Explanatory variable	**β coefficient**
Organism (level "plants")	-12.191
Latitude midpoint	-1.839
(Latitude midpoint)^2	1.175
Logarithm of focal area	-1.042

Finally I wanted to examine just the most suitable data from my data set. I used the categorical variable called *repetition* (abbreviation *rep*) that distinguishes the studies whose values are based on several measurets and final values are then mean values. These studies represent the ideal data for my analysis. At first I computed R^2 for MaxEnt prediction as usual. I obtained the value 0.056 that demonstrates the possibility of MaxEnt approach to explain 5.6% of variability of local slope values. The distribution of these values along the ln(*N/S*) gradient is depicted in figure 8.

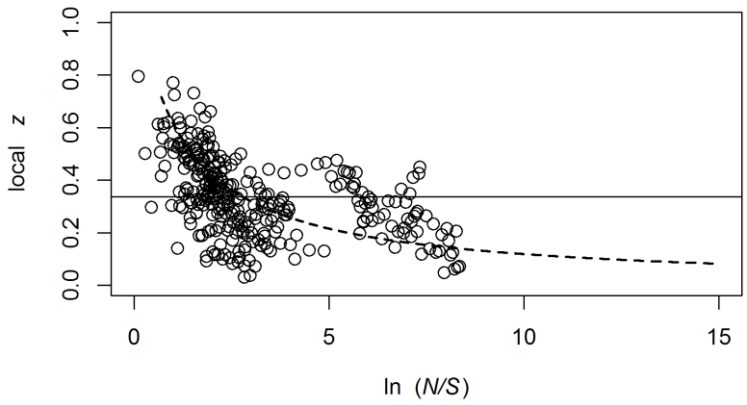

Figure 9 Illustration of local slopes obtained from the literature that are based on multiple measures (open circles) and MaxEnt based prediction by Harte *et al.* (2009) (dashed line); solid line represents the mean of local slope values that came from studies defined above.

I performed whole procedure of model selection again for the data based on repeated measures and I received the same combination of predictors in the final model.

iii. Residuals of overall slopes after fitting the prediction

I started with maximal model that encompassed all the main effects I wanted to include (*realm*, *organism*, *mean body mass*, *latitude midpoint*, *area range*, *logarithm of mean area*) and quadratic terms of continuous variables. Once again I merged several levels of *organism* (helminths, plants and zoobenthos) into one level. During the model simplification I removed following predictors in this order: quadratic term of logarithmically transformed *mean bodymass*, *realm* and quadratic term of *latitude midpoint.* I checked AIC values during the simplification so that AIC decreased in each step during the process. I used the same procedure in R as described in more detail in the section dedicated to overall slope.

Following table illustrates the output from R that summarizes the final model obtained by simplification. Meaning of table elements remains the same as in section devoted to overall slopes analysis.

```
Call:
lm(formula = residdig.std ~ lnbmass.std + latmid.std +
arange.std + org2 + lnmeana.std + arange.sq.std +
lnmeana.sq.std, data = sloper)


Residuals:
     Min       1Q   Median       3Q      Max
-1.48410 -0.49703 -0.01734  0.38704  1.41748

Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)             -1.6194     1.1054  -1.465 0.147352
lnbmass.std             -0.4501     0.1667  -2.700 0.008661 **
latmid.std              -0.2828     0.1904  -1.485 0.141921
arange.std               1.5880     0.3782   4.199 7.66e-05 ***
org2fungi                5.6900     1.3792   4.126 9.92e-05 ***
org2helm.plant.zoobent   1.6515     1.1606   1.423 0.159141
lnmeana.std              1.2945     0.4023   3.218 0.001949 **
arange.sq.std           -1.4581     0.3865  -3.773 0.000331 ***
lnmeana.sq.std          -0.5992     0.3982  -1.505 0.136852
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.6933 on 71 degrees of freedom
Multiple R-squared: 0.5681,     Adjusted R-squared: 0.5194
F-statistic: 11.67 on 8 and 71 DF,  p-value: 1.958e-10
```

This combination of predictors is able to explain nearly 57% of variability encompassed in *z* residuals after fitting the MaxEnt prediction.

As previously I set the importance of explanatory variables with help of comparison of changes in R^2 (R^2 of full model minus R^2 of adjusted model where one predictor is removed). I obtained the results that are listed in table 5.

Table 5 Comparison of the most influential variables (ranked according to ΔR^2) and their standardized regression coefficients (β coefficients). Quadratic terms of variables are indicated with upper indices.

Explanatory variable	ΔR^2
Organism	0.194
Area range	0.107
(Area range)^2	0.087
Logarithm of mean area	0.063
Logarithm of mean body mass	0.044
(Logarithm of mean area)^2	0.014
Latitude midpoint	0.013

Finally I enclosed the summary of standardized regression coefficients (β coefficients) for several of the most influential variables to show more clearly the effects of explanatory variables. For this summary, see table 6.

Table 6 β coefficients for several of the most influential explanatory variables.

Explanatory variable	β coefficient
Organism (level "fungi")	5.690
Organism (level "helmint.plant.zoobent")	1.652
Area range	1.588
(Area range)^2	-1.458
Logarithm of mean area	1.295
Logarithm of mean body mass	-1.619

iv. *K* parameter

As I mentioned in previous chapter I examined *K* parameter only with the predicted constraints. On the whole, data respected the predictions very well as you can see in the figure 10.

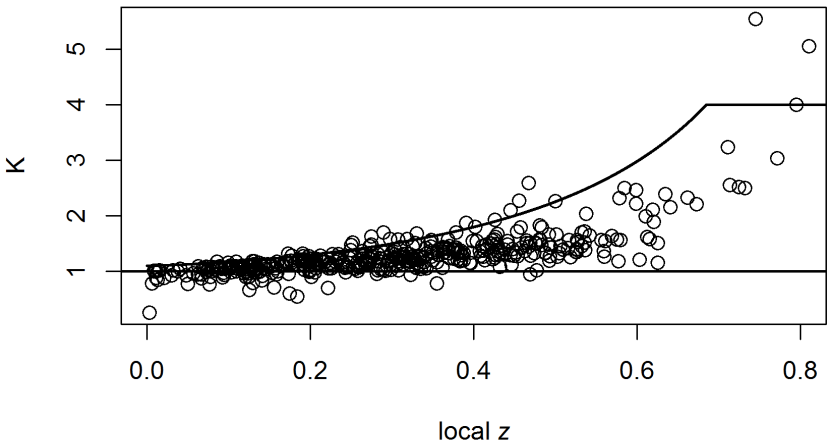

Figure 10 The relationship between *K* values and local slopes of SAR curves. Solid lines represent the constraints as described in Box1.

I repeated the same procedure as I described above even with the data that came from multiple measures studies. Resulting picture (figure 10) shows that these, more accurate data adhere to the constraints even more strictly.

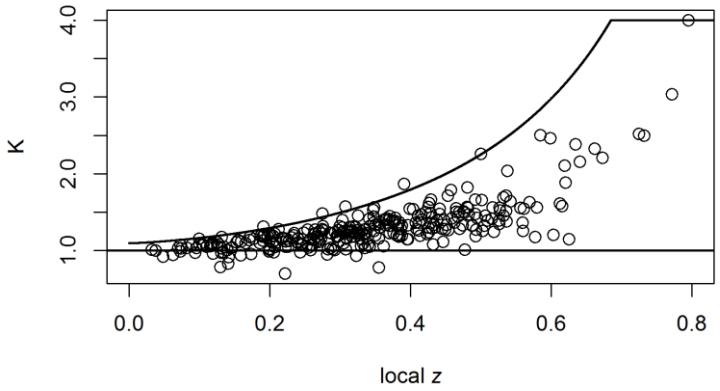

Figure 11 The relationship between *K* values and local slopes of SAR curves for data based on multiple measures. Solid lines represents the constraints as described in Box1.

5. Discussion

i. MaxEnt prediction and its fit on data

Contrary to my expectations, prediction by Harte *et al.* (2009) explained considerable portion of overall slopes variability (54%). However, this prediction was meant just for predicting local slopes of SAR curves thus we have to think about the factors that might cause this result. First possibility is the loss of some information during the process of linear regression when computing overall slope from the data points. This operation essentially leads to reducing the complexity (that is why we perform it in the first place) in data. I wanted to verify this idea by the comparison of variances between overall and local slopes. Surprisingly I received values that suggest roughly the same variance in both groups of data. I also checked the range of the values, where local slopes values tend to reveal slightly larger range. As we can see in the figure 7, the prediction nicely copies the main trend in the data but as there is big variance mainly in the interval $\ln(\frac{N}{S}) \in (\ln(2), 5)$ the fit of this prediction is just slightly better than fitting with the mean value line (and therefore R^2 is low). Even when I looked at the subset of data that was based on mean values obtained by several measures, the situation did not change too much. R^2 increased (from 0.0093 to 0.0560), but still the difference between the goodness of fit between overall and local slopes is immense. My data suggests that prediction which determines exact values does not seem to fit well on local slope data. Predictions that operate with constraints (instead of strict linear fits) would suit my data better. Similar approach can be seen in Šizling *et al.* (2011).

ii. Overall slope and its predictors

Linear combination of the predictors in final model was able to explain substantial portion of variability in overall slope values (R^2 = 83%). The most influential variable in my data set for overall slopes is *mean species abundance*. With increasing logarithm of *mean species abundance* overall slope decreases nonlinearily. This fact is in accord with MaxEnt prediction (Harte *et al.* 2009) as well as with geometrical approach (Šizling *et al.* 2011). The effect of *mean species abundance* has the biggest impact on the distribution of overall slopes which confirms our expectations. The second most important variable with distinctive effect on the slope is *organism*. I revealed significant differences among the levels “birds”, “fungi” and the third level comprising helminths, plants and zoobenthos. Birds have the lowest slope values whereas fungi (represented by single study) achieve highest slope value. Somewhere in between, merged group of helminths, plants and zoobenthos could be found. We might

assume that this fact could be associated with the relationship between dispersal abilities of particular groups (Amarasekare & Nisbet 2001; Hubbell 2001). Increased dispersal obviously leads to lower species turnover that is connected with lower slope values. Birds have relatively highest ability of dispersal in comparison with fungi and the merged group, obviously.

There is also important effect of *area range*. With increasing *area range* the rate of species accumulation with area increases. This finding is in contrast with my expectations. As we are operating on local and regional scales mainly I was expecting that with enlarging *area range* the overall slope would decrease. Negative relationship between *area range* and slope was detected for example by Drakare *et. al.* (2009).

iii. Local slope and its predictors

First thing that deserves comment is the variance distribution among the components. The fact that the variance of local slopes among the *studies* is <<1% of total variance suggests that local slope values are correlated among the papers rather slightly. Surprisingly, according to AIC comparison, linear mixed effect model with this hierarchical structure was preferred. About $^{2}/_{5}$ of variance consists among the *plots*. This is a confirmation of idea that local slopes originating from one SAR curve are more similar to each other than to slopes from other plots. Somehow it also confirms the choice of hierarchical structure in a model. Rest of the slope variance ($^{3}/_{5}$) could be attributed to the differences among all the local slopes itself. Most of the variability is therefore hidden directly within particular slopes. That might be interpreted as the fact that even within one single SAR curve there is a lot of differences in local slope values.

As I operated with linear mixed effect models and it is not that trivial to determine relative importance of the predictors in these models I used indirect measurement of their role in model. I used β coefficients that revealed *organism* as the most influential variable. It is a little bit surprising that effect of *organism* is still "visible" when the hierarchical structure is controlled for. We might assume that *plot* level testifies to organism group that is examined as well.

Another important variable in my analyses of local slopes is *focal area* that brings the information about the position on SAR curve, which is supposed to be triphasic (Hubbell 2001). My results suggest decrease of slope with increasing local area. Because my data

encompasse just the data points from local to regional spatial scale, it is in accordance with the triphasic behaviour of SAR that local slopes decrease this way.

iv. Residuals of overall slopes after fitting the prediction

After fitting the overall slope data with MaxEnt prediction I examined the residuals. I think that the results could be explained in two ways. At first it is informative what variables are the most influential after fitting by MaxEnt prediction (that is based on mean species abundance). As we know that the impact of *mean species abundance* is somehow linked with several variables, it is interesting that the most affecting variable in this analysis is *organism*. The second way of analysing the results is to look, how the residuals after fitting behave. As my results show, with increasing *area range* the residuals, and therefore variability of slopes increase. It is reasonable to expect that when we approximate SAR curve spanning large spatial scales with linear regression line there is higher variability in the values that leads to higher residual variance. Similar effect is connected with logarithm of *mean area.* Studies that have higher *mean area* values usually encompasse larger spatial scales.

v. *K* parameter

As we can see in graphically depicted distribution of *K* values (figures 9 and 10) the majority of data points respect the boundaries that were predicted. Operating just with data based on multiple measures improved the situation considerably. But still, several data points lie behind these lines. I tried to find some similarities that might connect these points but I was not successful as all the characteristics that I have at disposal differ throughout the singular values a lot.

6. Conclusion

As my aims were specified, I wanted to explore the relationship between the slopes of species-area curve (both overall and local) and mean species abundance. I managed to gather considerable amount of studies concerning SAR from which I extracted the data. I performed several analyses in which I analysed the impact of mean species abundance as well as other explanatory variables on the slope values of SAR. Besides finding the ideal combination of predictors in minimal adequate model I also examined a prediction on SAR slopes that is based on MaxEnt approach. I confirmed that mean species abundance is an important predictor for overall slopes and that MaxEnt prediction gives satisfiable results for overall slopes. On the other hand, the impact of mean species abundance on local slopes is negligible. Also the MaxEnt approach fails to predict local slopes.

Although I tried to gather all possible data that suit my conditions (mainly nested design) my data set reveals several imperfections. Firstly, its imbalance caused complications for analyses and it prevent simple adding of interaction responses to the models. Generally there is huge amount of data concerning SAR curves but most of it is linked to island problematic and it is quite complicated to find some papers based on nested design approach. Another difficulty emerged during accessing the information about mean species abundances. Most of the studies did not offer these values, so I was forced to abandon these studies.

I suppose that this data set could be analysed in several other ways to provide other insights into this problematics. It would be helpful if more studies with nested design were undertaken.

As a local slope problematic is still a subject of recent discussion, further examination could shed a light on that. For sure, there is a distinctive impact of mean species abundance on SAR curve slope but we need to figure out the exact way how it influence the shape of SARs.

7. List of abbreviations, coefficients and marks

AIC – Akaike information criterion

β coefficient – standardized regression coefficient

D – distance between IAR and SAR, ln $\left(\frac{N}{S}\right)$

Dbh – diameter at breast height, common dendrometric measurement

ΔR^2 – change in R^2

ε – ratio between areas of two following sites

g – gram

IAR – individuals-area relationship

J – Jaccard index, percentage of species shared by two assemblages

ML – maximum likelihood estimation

n, *n+1*- lower indices referring to the mutual position of the sites whereas *n* indicates smaller area site and n+*1* refers to the following (larger) site

N – total number of individuals

NA – missing values, not available

N/S – mean species abundance

r – Pearson's correlation coefficient

R^2 – coefficient of determination

REML – rrestricted maximum likelihood estimation

S – total number of species

Sq m – square metre

SA – species-area

SAR – species-area relationship

z – overall slope of species-area curve in log-log space

z_{loc} – local slope of species-area curve in log-log space

Abbreviations used in analyses (can be found in R outputs):

.sq.std – extension labelling standardized quadratic term of continuous variable

.std – extension labelling standardized variable

adjdata – adjusted data set (removed 2 most influencing data points)

arrange – area range (in analyses concerning overall slope)

locz – local slope of SAR curve in log-log space

latmid – latitude midpoint

lnarea – logarithm of focal area (in analyses concerning local slope)

lnbmass – logarithm of mean body mass

lnmeana – logarithm of mean area (in analyses concerning overall slope)

lnNS – logarithm of mean species abundance

locz – local slope of SAR curve in log-log space

locsloper – data set for analzsing local slope (based on the table in Appendix B)

org – organism (categorical variable)

org2 – organism (merged levels helminths, plants, zoobenthos)

plot – categorical variable denoting the affiliation of local slope values to a SAR curve (plot)

residdig – residuals of overall slope values after fitting MaxEnt prediction (digitized values)

sloper – data set for analysing overall slope (based on the table in Appendix A)

stud – categorical variable denoting the affiliation of SAR curve (plot) to a study (paper)

z – overall slope of SAR curve in log-log space

8. References

Allen A.P. & White E.P. (2003). Effects of range size on species-area relationships. *Evol. Ecol. Res.*, **5** (4): 493-499.

Amarasekare P. & Nisbet R.M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am. Nat.*, **158** (6): 572-584.

Arrhenius O. (1921). Species and area. *J. Ecol.*, **9**: 95-99.

Cagnolo L., Valladares G., Salvo A., Cabido M. & Zak M. (2009). Habitat fragmentation and species loss across three interacting trophic levels: Effects of life-history and food-web traits. *Conserv. Biol.*, **23** (5): 1167-1175.

Condit R., Ashton P.S., Baker P., Bunyavejchewin S., Gunatilleke S., Gunatilleke N., Hubbell S.P., Foster R.B., Itoh A., LaFrankie J.V., Lee H.S., Losos E., Manokaran N., Sukumar R. & Yamakura T. (2000). Spatial patterns in the distribution of tropical tree species. *Science*, **288** (5470): 1414-1418.

Connor E.F. & McCoy E.D. (1979). Statistics and biology of the species-area relationship. *Am. Nat.*, **113** (6): 791-833.

Connor E.F. & McCoy E.D. (2001). Species-area relationships. In: *Encyclopedia of Biodiversity*. Academic Press San Diego, pp. 397-412.

Crawley M.J. (2007). *The R book*. John Wiley & Sons, Ltd.

Currie D.J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137** (1): 27-49.

De Bello F., Leps J. & Sebastia M.T. (2007). Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. *J. Veg. Sci.*, **18** (1): 25-34.

Dengler J. (2008). Pitfalls in small-scale species-area sampling and analysis. *Folia Geobotanica*, **43** (3): 269-287.

Dengler J. (2009). Which function describes the species-area relationship best? A review and empirical evaluation. *J. Biogeogr.*, **36** (4): 728-744.

Drakare S., Lennon J.J. & Hillebrand H. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecol. Lett.*, **9** (2): 215-227.

Franzen M., Schweiger O. & Betzholtz P.E. (2012). Species-area relationships are controlled by species traits. *PLoS One*, **7** (5).

Gleason H.A. (1922). On the relation between species and area. *Ecology*, **3**: 158-162.

Greenacre M. & Hastie T. (1987). The geometric interpretation of correspondence analysis. *Journal of the American Statistical Association*, **82** (398): 437-447.

Harte J., Kinzig A. & Green J. (1999). Self-similarity in the distribution and abundance of species. *Science*, **284** (5412): 334-336.

Harte J., Kitzes J., Newman E.A. & Rominger A.J. (2013). Taxon categories and the universal species-area relationship (A comment on Sizling et al., "Between geometry and biology: The problem of universality of the species-area relationship"). *Am. Nat.*, **181** (2): 282-287.

Harte J., Smith A.B. & Storch D. (2009). Biodiversity scales from plots to biomes with a universal species-area curve. *Ecol. Lett.*, **12** (8): 789-797.

Hillebrand H., Watermann F., Karez R. & Berninger U.G. (2001). Differences in species richness patterns between unicellular and multicellular organisms. *Oecologia*, **126** (1): 114-124.

Holt R.D., Lawton J.H., Polis G.A. & Martinez N.D. (1999). Trophic rank and the species-area relationship. *Ecology*, **80** (5): 1495-1504.

Hubbell S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Huwaldt J.A. (2012) Plot Digitizer 2.6.0.

Chiarucci A., Viciani D., Winter C. & Diekmann M. (2006). Effects of productivity on species-area curves in herbaceous vegetation: evidence from experimental and observational data. *Oikos*, **115** (3): 475-483.

Jaccard P. (1901). Distribution de la flore alpine dans le bassin des Dranses et dans quelques régions voisines. *Bulletin de la Société Vaudoise des Sciences Naturelles*, **37**: 241-272.

Leitner W.A. & Rosenzweig M.L. (1997). Nested species-area curves and stochastic sampling: A new theory. *Oikos*, **79** (3): 503-512.

Lennon J.J., Kunin W.E. & Hartley S. (2002). Fractal species distributions do not produce power-law species-area relationships. *Oikos*, **97** (3): 378-386.

MacArthur R.H. (1965). Patterns of species diversity. *Biological Reviews*, **40** (4): 510-533.

MacArthur R.H. & Wilson E.O. (1976). *The theory of island biogeography*. Princeton University Press, Princeton.

Martin T.E. (1981). Species-area slopes and coefficients - A caution on their interpretation. *Am. Nat.*, **118** (6): 823-837.

McArdle B.H., Gaston K.J. & Lawton J.H. (1990). Variation in the size of animal populations: Patterns, problems and artefacts. *J Anim Ecol*, **59** (2): 439-454.

Palmer M.W. & White P.S. (1994). Scale dependence and the species-area relationship. *The American Naturalist*, **144** (5): 717-740.

Pekár S. & Brabec M. (2009). *Moderní analýza biologických dat, Zobecněné lineární modely v prostředí R*. Scientia, Praha.

Pekár S. & Brabec M. (2012). *Moderní analýza biologických dat, Lineární modely s korelacemi v prostředí R*. Masarykova univerzita, Brno.

Pinheiro J., Bates D., DebRoy S., Sarkar D. & R development Core Team (2012) nlme: Linear and nonlinear mixed effects models R package version 3.1-105

Preston F.W. (1948). The commonness, and rarity, of species. *Ecology*, **29** (3): 254-283.

Preston F.W. (1960). Time and space and the variation of species. *Ecology*, **41** (4): 611-627.

Preston F.W. (1962a). The canonical distribution of commonness and rarity: Part I. *Ecology*, **43** (2): 185-215.

Preston F.W. (1962b). The canonical distribution of commonness and rarity: Part II. *Ecology*, **43** (3): 410-&.

Qian H., Fridley J.D. & Palmer M.W. (2007). The latitudinal gradient of species-area relationships for vascular plants of North America. *Am. Nat.*, **170** (5): 690-701.

Qian H. & Ricklefs R.E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecol. Lett.*, **10** (8): 737-744.

R Development Core Team (2008) R: A language and environment for statistical computing 2.15.2

Ricotta C., Carranza M.L. & Avena G. (2002). Computing β-diversity from species-area curves. *Basic and Applied Ecology*, **3** (1): 15-18.

Ripley B. (2013) tree: Classification and regression trees R package version 1.0-34

Rodriguez P. & Arita H.T. (2004). Beta diversity and latitude in North American mammals: testing the hypothesis of covariation. *Ecography*, **27** (5): 547-556.

Rosenzweig M.L. (1995). *Species diversity in space and time*. Cambridge University Press, Cambridge.

Rosindell J. & Cornell S.J. (2007). Species-area relationships from a spatially explicit neutral model in an infinite landscape. *Ecol. Lett.*, **10** (7): 586-595.

RStudio Inc. (2012) RStudio: Integrated development environment for R 0.97.248

Shmida A. & Wilson M.V. (1985). Biological determinants of species-diversity. *J. Biogeogr.*, **12** (1): 1-20.

Scheiner S.M. (2003). Six types of species-area curves. *Glob. Ecol. Biogeogr.*, **12** (6): 441-447.

Storch D., Evans K.L. & Gaston K.J. (2005). The species-area-energy relationship. *Ecol. Lett.*, **8** (5): 487-492.

Storch D., Keil P. & Jetz W. (2012). Universal species-area and endemics-area relationships at continental scales. *Nature*, **488** (7409): 78-+.

Storch D., Sizling A.L., Azaele S., Cornell S. & Kunin W.E. (unpublished). Biodiversity scaling for beginners: What have we learned so far about the species-area relationship and species' spatial distributions.

Storch D., Sizling A.L., Reif J., Polechova J., Sizlingova E. & Gaston K.J. (2008). The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecol. Lett.*, **11** (8): 771-784.

Storch D., Šizling A.L. & Gaston K.J. (2003). Geometry of the species-area relationship in central European birds: testing the mechanism. *J Anim Ecol*, **72** (3): 509-519.

Systat Software inc. (2002) TableCurve 2D 5.01

Šizling A.L., Kunin W.E., Sizlingova E., Reif J. & Storch D. (2011). Between geometry and biology: The problem of universality of the species-area relationship. *Am. Nat.*, **178** (5): 602-611.

Šizling A.L., Kunin W.E. & Storch D. (2013). Taxon-and-area invariances, maximum entropy, and the species-area relationship (A reply to Harte et al.). *Am. Nat.*, **181** (2): 288-290.

Šizling A.L. & Storch D. (2004). Power-law species-area relationships and self-similar species distributions within finite areas. *Ecol. Lett.*, **7** (1): 60-68.

Taylor L.R., Woiwod I.P. & Perry J.N. (1978). The density-dependence of spatial behaviour and the rarity of randomness. *J Anim Ecol*, **47** (2): 383-406.

Taylor L.R., Woiwod I.P. & Perry J.N. (1979). The negative binomial as a dynamic ecological model for aggregation, and the density dependence of k. *J Anim Ecol*, **48** (1): 289-304.

Tjorve E. (2003). Shapes and functions of species-area curves: a review of possible models. *J. Biogeogr.*, **30** (6): 827-835.

Tjorve E. (2009). Shapes and functions of species-area curves (II): a review of new models and parameterizations. *J. Biogeogr.*, **36** (8): 1435-1445.

Ulrich W. & Buszko J. (2007). Sampling design and the shape of species–area curves on the regional scale. *Acta Oecologica*, **31** (1): 54-59.

Wright D.H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, **41** (3): 496-506.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. & Smith G.M. (2009). *Mixed effects models and extensions in ecology in R*. Springer, New York.

9. Appendix A

Appendix A List of the studies that I used for data mining of overal slopes with several characteristics; units are listed in square bracket; repetition refers to method of data obtaining (rep = 1 means that slope values are based on multiple measurments of number of species on the same area size); note brings information about the particular part of paper or book where I found SAR curve or informs about the method of computing the abundance value

Reference	Slope (z)	Number of individuals (N)	Number of species (S)	ln(N/S)	Realm	Organism	Body mass [g]	Latitude midpoint	Area range	Min A [sq m]	Max A [sq m]	Mean A [sq m]	Repetition	Note
Billings W.D. (1938)	**0.23**	1894.50	22.00	4.46	ter	plants	10	36	0.60	1.0100	4.00	2.02	1	herbaceous, table 3
	0.20	3877.00	39.00	4.60	ter	plants	2000	36	1.21	1.0100	16.20	3.40	1	shrub, table 2
	0.36	2664.00	21.00	4.84	ter	plants	44000	36	2.00	1.0100	101.10	6.70	1	arborescent, table 1
Cao Y., Williams D.D. & Larsen D.P. (2002)	**0.50**	183.00	23.00	2.07	aqu	zoobenthos	0.026	62	1.39	0.0281	0.69	0.28	1	PUR - J
	0.25	440.00	12.00	3.60	aqu	zoobenthos	0.026	62	1.41	0.0281	0.72	0.29	1	PAA-J
	0.45	260.00	23.00	2.43	aqu	zoobenthos	0.026	62	1.41	0.0281	0.73	0.29	1	HAU-J
	0.17	72103.00	16.00	8.41	aqu	zoobenthos	0.026	53	1.40	1.9200	48.00	19.65	1	site 3
	0.30	39210.00	25.00	7.36	aqu	zoobenthos	0.026	53	1.40	1.9200	48.00	19.58	1	site 2
	0.40	17159.00	36.00	6.17	aqu	zoobenthos	0.026	53	1.40	1.9200	48.00	19.61	1	site 1
Condit R., Hubbell S.P.,Lafrankie J.V., Sukumar R., Manokaran N., Foster R.B. & Ashton P.S. (1996)	**0.33**	25690.00	71.00	5.89	ter	plants	44000	11.6	3.10	400.0000	500000.00	5835.34	1	Mudumalai
	0.25	335100.00	817.00	6.02	ter	plants	44000	3	3.10	400.0000	500000.00	5835.34	1	Pasoh
	0.23	244090.00	303.00	6.69	ter	plants	44000	9.2	3.10	400.0000	500000.00	5835.34	1	BCI
Eggeling W.J. (1947)	**0.37**	471.00	18.00	3.26	ter	plants	44000	2	0.60	3720.0000	14900.00	8215.91	1	IRONWOOD
	0.34	597.00	36.00	2.81	ter	plants	44000	2	0.60	3720.0000	14900.00	8266.04	1	COLONIZING

	0.50	562.00	80.00	1.95	ter	plants	44000	2	0.60	3720.0000	14900.00	8309.04	0	SWAMP
	0.37	684.50	55.00	2.52	ter	plants	44000	2	0.60	3720.0000	14900.00	8278.46	1	MIXED
Hylleberg J., Nateewathana A. & Chatananthawej B. (1985)	**0.55**	167.00	28.00	1.79	aqu	helminths	0.0003	8	1.20	0.1000	1.60	0.68	0	
Kassas M. (1953)	**0.48**	1824.00	23.00	4.37	ter	plants	10	30	2.12	30.0000	4000.00	942.28	0	stand A
Magnussen E. (2002)	**0.20**	42755.00	61.00	6.55	aqu	fishes	270	61	NA	NA	NA	NA	1	N computed with data from Magnussen E. & Magnussen M.D. (2009)
Nesheim I., Halvorsen R. & Nordal I. (2010)	**0.39**	3859.00	148.00	3.26	ter	plants	7000	17	1.40	100.0000	2500.00	1018.98	0	R1, bodymass value computed as weighted mean, for bodymass of vines used data from Putz, F.E. (1983)
	0.56	3766.00	147.00	3.24	ter	plants	7000	17	1.40	100.0000	2500.00	1028.48	0	R2, bodymass value computed as weighted mean, for bodymass of vines used data from Putz, F.E. (1983)
	0.40	3751.00	136.00	3.32	ter	plants	7000	17	1.40	100.0000	2500.00	1021.11	0	L3, bodymass value computed as weighted mean, for bodymass of vines used data

													from Putz, F.E. (1983)
	0.39	3679.00	177.00	3.03	ter	plants	7000	17	1.40	100.0000	2500.00	1018.28	0	L4, bodymass value computed as weighted mean, for bodymass of vines used data from Putz, F.E. (1983)
	0.34	3725.00	166.00	3.11	ter	plants	7000	17	1.40	100.0000	2500.00	1018.82	0	S5, bodymass value computed as weighted mean, for bodymass of vines used data from Putz, F.E. (1983)
Paijmans K. (1970)	**0.57**	528.00	122.00	1.47	ter	plants	44000	-7	1.35	360.0000	8020.00	3325.46	0	sp1
	0.80	560.00	148.00	1.33	ter	plants	44000	-7	1.35	360.0000	8020.00	3321.58	0	sp2
	0.69	426.00	145.00	1.08	ter	plants	44000	-7	1.35	360.0000	8020.00	3324.78	0	sp3
	0.78	348.00	116.00	1.10	ter	plants	44000	-7	1.35	360.0000	8020.00	3321.88	0	sp4
Parthasarathy N. & Karthikeyan R. (1997)	**0.53**	482.00	57.00	2.13	ter	plants	44000	8.9	2.00	100.0000	10000.00	3365.88	0	
Parthasarathy N. (1999)	**0.50**	575.00	80.00	1.97	ter	plants	44000	8.5	1.00	1000.0000	10000.00	4529.13	1	FD
	0.38	855.00	83.00	2.33	ter	plants	44000	8.5	1.00	1000.0000	10000.00	4539.72	1	SF
	0.46	720.00	85.00	2.14	ter	plants	44000	8.5	1.00	1000.0000	10000.00	4542.28	1	UD
Pastor J., Downing A. & Erickson H.E. (1996)	**0.19**	467.10	18.00	3.26	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.19	294.30	10.00	3.38	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.20	486.00	16.00	3.41	ter	plants	10	48.5	1.56	0.2500	9.00	1.72	0	
	0.21	344.70	14.00	3.20	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.21	554.40	16.00	3.55	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	

	0.24	396.90	16.00	3.21	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.24	337.50	10.00	3.52	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.27	569.70	13.00	3.78	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.32	387.00	16.00	3.19	ter	plants	10	48.5	1.56	0.2500	9.00	1.70	0	
	0.36	384.30	17.00	3.12	ter	plants	10	48.5	1.56	0.2500	9.00	1.70	0	
	0.37	297.00	11.00	3.30	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
	0.42	337.50	14.00	3.18	ter	plants	10	48.5	1.56	0.2500	9.00	1.69	0	
Poore M.E.D. (1964)	**0.65**	791.00	210.00	1.33	ter	plants	44000	2	1.76	277.0000	16100.00	6312.30	0	Sungei Menyala, Malaya,fig 4c, trees over 4 in. diameter
Proctor J., Anderson J.M., Chai P. & Vallack H.W. (1983)	**0.82**	615.00	224.00	1.01	ter	plants	44000	3	1.40	400.0000	10000.00	4029.74	0	AF
	0.67	644.00	73.00	2.18	ter	plants	44000	3	1.40	400.0000	10000.00	4033.19	0	FoL
	0.72	778.00	214.00	1.29	ter	plants	44000	3	1.40	400.0000	10000.00	4053.03	0	DF
	0.62	708.00	124.00	1.74	ter	plants	44000	3	1.40	400.0000	10000.00	4034.13	0	HF
Rice E.L. (1952)	**0.40**	295.60	28.00	2.36	ter	plants	10	33.6	1.30	0.1000	2.00	0.83	0	for S see fig1 and fig2, N computed with biomass values from Bruner, W.E. (1931)
Richards P.W. (1939)	**0.40**	781.00	42.00	2.92	ter	plants	44000	7	0.57	4000.0000	15000.00	8214.17	1	mixed 2
	0.39	536.00	38.00	2.65	ter	plants	44000	7	0.57	4000.0000	15000.00	8212.59	1	fresh-water (sp4)
	0.52	582.00	70.00	2.12	ter	plants	44000	6.3	0.57	4000.0000	15000.00	8243.59	1	mixed 3
Storch D., Šizling A.L. & Gaston K.J. (2003)	**0.11**	1029966.00	186.00	8.62	ter	birds	450	49	2.16	133200.0000	19180000.00	3688600.80	0	region 1, N computed with data from Šťastný K. & Bejček V. (1993)

	0.12	1029966.00	196.00	8.57	ter	birds	450	49	2.16	133200.0000	19180000.00	3681994.60	0	region 2, N computed with data from Šťastný K. & Bejček V. (1993)
	0.10	1029966.00	190.00	8.60	ter	birds	450	49	2.16	133200.0000	19180000.00	3710357.00	0	region 3, N computed with data from Šťastný K. & Bejček V. (1993)
	0.05	455680000.00	209.00	14.59	ter	birds	450	49	2.41	2500000.0000	640000000.00	116118932.00	0	central European, N computed with data from Bohning-Gaese K. & Bauer H.-G. (1996)
Tanner E.V.J. (1977)	**0.27**	392.00	16.00	3.20	ter	plants	44000	18	0.96	87.0000	798.00	361.00	0	mor ridge
	0.50	270.00	26.00	2.34	ter	plants	44000	18	1.05	87.0000	982.00	447.75	0	gap
	0.36	360.00	34.00	2.36	ter	plants	44000	18	1.03	92.0000	987.00	449.77	0	wet slope
	0.52	520.00	34.00	2.73	ter	plants	44000	18	1.08	87.0000	1040.00	432.96	0	mull ridge
Vaughan R.E. & Wiehe P.O. (1941)	**0.37**	3838.00	79.00	3.88	ter	plants	10	-20	2.70	2.0000	1000.00	59.11	1	sideroxylon
	0.43	2206.00	30.00	4.30	ter	plants	10	-20	2.70	2.0000	1000.00	68.52	1	heath
	0.49	1785.00	70.00	3.24	ter	plants	10	-20	2.70	2.0000	1000.00	62.76	1	upland
Wang X.G., Hao Z.Q., Ye J., Zhang J., Li B.H. & Yao X.L. (2008)	**0.19**	38902.00	52.00	6.62	ter	plants	44000	42	3.10	20.0000	25000.00	4068.41	0	design d, trees - over 1 cm dbh
Weiher E. (1999)	**0.10**	1920.00	29.00	4.19	aqu	plants	10	45	2.78	0.2500	150.00	8.27	0	westmeath low
	0.15	3165.00	28.00	4.73	aqu	plants	10	45	2.78	0.2500	150.00	8.31	0	westmeath interm.
	0.21	6990.00	36.00	5.27	aqu	plants	10	45	2.78	0.2500	150.00	8.22	0	lucerne blvd

	0.16	6840.00	30.00	5.43	aqu	plants	10	45	2.78	0.2500	150.00	8.29	0	andrew low
	0.17	12735.00	43.00	5.69	aqu	plants	10	45	2.78	0.2500	150.00	8.40	0	luskville high
	0.23	5820.00	28.00	5.34	aqu	plants	10	45	2.78	0.2500	150.00	8.40	0	luskville interm.
	0.21	7695.00	38.00	5.31	aqu	plants	10	45	2.78	0.2500	150.00	8.30	0	westmeath high
	0.26	9195.00	31.00	5.69	aqu	plants	10	45	2.78	0.2500	150.00	8.29	0	andrew interm.
	0.34	15750.00	28.00	6.33	aqu	plants	10	45	2.78	0.2500	150.00	8.30	0	andrew high
	0.22	2745.00	23.00	4.78	aqu	plants	10	45	2.78	0.2500	150.00	8.36	0	luskville low
Weinberg S. (1978)	**0.15**	192.00	7.00	3.31	aqu	zoobenthos	0.026	42.5	0.99	0.0409	0.40	0.18	1	sample 22
	0.17	397.00	17.00	3.15	aqu	zoobenthos	0.026	42.5	1.03	0.2350	2.50	1.13	1	sample 10
	0.32	70.00	8.00	2.17	aqu	zoobenthos	0.026	42.5	1.00	0.0407	0.40	0.18	1	sample 3
	0.33	274.00	11.00	3.22	aqu	zoobenthos	0.026	42.5	1.02	0.2410	2.50	1.13	1	sample 13
	0.28	165.00	14.00	2.47	aqu	zoobenthos	0.026	42.5	1.03	0.2320	2.50	1.13	1	sample 27
Yamada A. & Katsuya K. (2001)	**0.74**	960.00	40.00	3.18	ter	fungi	100	36.1	2.80	0.0010	625.00	0.73	1	fruit bodies fungi

10.Appendix B

Appendix B List of studies I operated with while analysing local slopes; units are listed in square brackets; note refers to particular study plot within the study; other labels are described in more detail in the text.

Reference	Local slope (z)	Number of individuals (N)	Number of species (S)	ln(N/S)	Realm	Organism	Body mass [g]	Latitude midpoint	Area [sq m]	Epsilon (ε)	Jn	Kn	Note
Billings W.D. (1938)	**0.585**	26.595	4.000	1.894	ter	plants	44000.000	36.000	1.010	2.000	0.333	2.501	arborescent (table 1)
	0.222	53.190	6.000	2.182	ter	plants	44000.000	36.000	2.020	2.005	0.715	0.699	arborescent (table 1)
	0.500	106.644	7.000	2.724	ter	plants	44000.000	36.000	4.050	3.998	0.333	2.258	arborescent (table 1)

	0.348	241.863	22.000	2.397	ter	plants	2000.000	36.000	1.010	2.000	0.571	1.563	shrub (table 2)
	0.146	483.727	28.000	2.849	ter	plants	2000.000	36.000	2.020	2.005	0.807	1.043	shrub (table 2)
	0.248	472.456	16.000	3.385	ter	plants	10.000	36.000	1.010	2.000	0.684	1.231	herbaceous (table 3)
Cao Y., Williams D.D. & Larsen D.P. (2002)	**0.275**	21.376	4.356	1.591	aqu	zoobenthos	0.026	62.000	0.028	2.009	0.652	1.320	PAA-O
	0.209	42.936	5.278	2.096	aqu	zoobenthos	0.026	62.000	0.055	1.521	0.755	1.135	PAA-O
	0.223	65.292	5.760	2.428	aqu	zoobenthos	0.026	62.000	0.084	1.354	0.750	1.120	PAA-O
	0.254	88.423	6.163	2.664	aqu	zoobenthos	0.026	62.000	0.114	1.253	0.725	1.272	PAA-O
	0.134	110.785	6.526	2.832	aqu	zoobenthos	0.026	62.000	0.143	1.202	0.855	0.978	PAA-O
	0.267	133.158	6.688	2.991	aqu	zoobenthos	0.026	62.000	0.172	1.168	0.718	1.178	PAA-O
	0.255	155.524	6.971	3.105	aqu	zoobenthos	0.026	62.000	0.201	1.144	0.732	1.042	PAA-O
	0.370	177.892	7.214	3.205	aqu	zoobenthos	0.026	62.000	0.229	1.126	0.617	1.324	PAA-O
	0.299	200.257	7.537	3.280	aqu	zoobenthos	0.026	62.000	0.258	1.112	0.689	1.320	PAA-O
	0.159	222.625	7.780	3.354	aqu	zoobenthos	0.026	62.000	0.287	1.104	0.835	0.938	PAA-O
	0.347	245.772	7.903	3.437	aqu	zoobenthos	0.026	62.000	0.317	1.091	0.643	1.443	PAA-O
	0.131	268.139	8.145	3.494	aqu	zoobenthos	0.026	62.000	0.346	1.081	0.865	0.975	PAA-O
	0.264	289.745	8.228	3.561	aqu	zoobenthos	0.026	62.000	0.374	1.077	0.729	1.211	PAA-O
	0.204	312.119	8.391	3.616	aqu	zoobenthos	0.026	62.000	0.402	1.074	0.791	1.102	PAA-O
	0.222	335.264	8.514	3.673	aqu	zoobenthos	0.026	62.000	0.432	1.067	0.772	1.053	PAA-O
	0.308	357.638	8.637	3.723	aqu	zoobenthos	0.026	62.000	0.461	1.063	0.686	1.174	PAA-O
	0.321	380.012	8.800	3.765	aqu	zoobenthos	0.026	62.000	0.490	1.059	0.673	1.183	PAA-O
	0.333	402.384	8.963	3.804	aqu	zoobenthos	0.026	62.000	0.519	1.056	0.661	1.093	PAA-O
	0.428	424.758	9.126	3.840	aqu	zoobenthos	0.026	62.000	0.548	1.053	0.565	1.489	PAA-O
	0.268	447.127	9.329	3.870	aqu	zoobenthos	0.026	62.000	0.577	1.050	0.727	1.158	PAA-O
	0.269	469.501	9.452	3.905	aqu	zoobenthos	0.026	62.000	0.605	1.049	0.726	1.132	PAA-O
	0.297	492.649	9.575	3.941	aqu	zoobenthos	0.026	62.000	0.635	1.044	0.698	1.188	PAA-O
	0.287	514.252	9.698	3.971	aqu	zoobenthos	0.026	62.000	0.663	1.045	0.709	1.033	PAA-O
	0.141	16.179	5.355	1.106	aqu	zoobenthos	0.026	62.000	0.026	2.125	0.809	0.917	PAA-J
	0.362	34.381	5.957	1.753	aqu	zoobenthos	0.026	62.000	0.056	1.511	0.589	1.401	PAA-J

0.268	51.961	6.919	2.016	aqu	zoobenthos	0.026	62.000	0.085	1.339	0.703	1.187	PAA-J
0.263	69.558	7.481	2.230	aqu	zoobenthos	0.026	62.000	0.114	1.244	0.716	1.220	PAA-J
0.209	86.552	7.923	2.391	aqu	zoobenthos	0.026	62.000	0.142	1.210	0.775	1.103	PAA-J
0.240	104.766	8.246	2.542	aqu	zoobenthos	0.026	62.000	0.172	1.174	0.746	1.106	PAA-J
0.285	122.980	8.569	2.664	aqu	zoobenthos	0.026	62.000	0.201	1.138	0.701	1.233	PAA-J
0.227	139.979	8.891	2.756	aqu	zoobenthos	0.026	62.000	0.229	1.126	0.762	1.125	PAA-J
0.240	157.589	9.134	2.848	aqu	zoobenthos	0.026	62.000	0.258	1.116	0.750	1.158	PAA-J
0.224	175.807	9.377	2.931	aqu	zoobenthos	0.026	62.000	0.288	1.100	0.767	1.153	PAA-J
0.200	193.419	9.580	3.005	aqu	zoobenthos	0.026	62.000	0.317	1.088	0.793	1.025	PAA-J
0.306	210.424	9.743	3.073	aqu	zoobenthos	0.026	62.000	0.345	1.084	0.685	1.224	PAA-J
0.270	228.034	9.986	3.128	aqu	zoobenthos	0.026	62.000	0.373	1.077	0.722	1.249	PAA-J
0.173	245.646	10.188	3.183	aqu	zoobenthos	0.026	62.000	0.402	1.072	0.822	0.954	PAA-J
0.348	263.261	10.311	3.240	aqu	zoobenthos	0.026	62.000	0.431	1.069	0.644	1.256	PAA-J
0.314	281.479	10.554	3.284	aqu	zoobenthos	0.026	62.000	0.461	1.063	0.680	1.305	PAA-J
0.199	299.090	10.757	3.325	aqu	zoobenthos	0.026	62.000	0.490	1.059	0.797	0.991	PAA-J
0.341	316.706	10.880	3.371	aqu	zoobenthos	0.026	62.000	0.519	1.056	0.652	1.414	PAA-J
0.141	334.317	11.083	3.407	aqu	zoobenthos	0.026	62.000	0.548	1.055	0.856	0.832	PAA-J
0.441	352.542	11.166	3.452	aqu	zoobenthos	0.026	62.000	0.577	1.050	0.553	1.478	PAA-J
0.305	370.151	11.409	3.479	aqu	zoobenthos	0.026	62.000	0.606	1.048	0.690	1.242	PAA-J
0.246	387.764	11.572	3.512	aqu	zoobenthos	0.026	62.000	0.635	1.044	0.750	1.080	PAA-J
0.314	404.771	11.695	3.544	aqu	zoobenthos	0.026	62.000	0.663	1.045	0.681	1.244	PAA-J
0.613	7.545	4.117	0.606	aqu	zoobenthos	0.026	62.000	0.029	1.970	0.310	1.614	PUR-J
0.620	14.864	6.236	0.869	aqu	zoobenthos	0.026	62.000	0.056	1.493	0.333	1.887	PUR-J
0.505	22.190	7.997	1.021	aqu	zoobenthos	0.026	62.000	0.084	1.342	0.459	1.322	PUR-J
0.536	29.788	9.278	1.166	aqu	zoobenthos	0.026	62.000	0.113	1.264	0.435	1.515	PUR-J
0.487	37.648	10.519	1.275	aqu	zoobenthos	0.026	62.000	0.143	1.188	0.491	1.330	PUR-J
0.493	44.727	11.441	1.363	aqu	zoobenthos	0.026	62.000	0.169	1.193	0.485	1.187	PUR-J
0.580	53.379	12.483	1.453	aqu	zoobenthos	0.026	62.000	0.202	1.142	0.404	1.560	PUR-J

0.526	60.982	13.484	1.509	aqu	zoobenthos	0.026	62.000	0.231	1.116	0.461	1.391	PUR-J
0.516	68.062	14.286	1.561	aqu	zoobenthos	0.026	62.000	0.258	1.112	0.471	1.415	PUR-J
0.488	75.668	15.088	1.612	aqu	zoobenthos	0.026	62.000	0.287	1.101	0.500	1.323	PUR-J
0.495	83.276	15.810	1.662	aqu	zoobenthos	0.026	62.000	0.315	1.095	0.494	1.426	PUR-J
0.446	91.146	16.532	1.707	aqu	zoobenthos	0.026	62.000	0.345	1.083	0.544	1.114	PUR-J
0.556	98.755	17.134	1.752	aqu	zoobenthos	0.026	62.000	0.374	1.077	0.435	1.557	PUR-J
0.480	106.363	17.856	1.784	aqu	zoobenthos	0.026	62.000	0.403	1.072	0.511	1.569	PUR-J
0.323	113.972	18.459	1.820	aqu	zoobenthos	0.026	62.000	0.432	1.069	0.670	0.935	PUR-J
0.537	121.848	18.861	1.866	aqu	zoobenthos	0.026	62.000	0.461	1.060	0.456	1.383	PUR-J
0.532	129.195	19.463	1.893	aqu	zoobenthos	0.026	62.000	0.489	1.059	0.460	1.693	PUR-J
0.355	136.805	20.066	1.920	aqu	zoobenthos	0.026	62.000	0.518	1.058	0.639	0.782	PUR-J
0.662	144.681	20.468	1.956	aqu	zoobenthos	0.026	62.000	0.548	1.051	0.333	2.329	PUR-J
0.362	152.026	21.150	1.972	aqu	zoobenthos	0.026	62.000	0.576	1.054	0.632	1.056	PUR-J
0.493	160.165	21.553	2.006	aqu	zoobenthos	0.026	62.000	0.607	1.046	0.501	1.271	PUR-J
0.527	167.514	22.035	2.028	aqu	zoobenthos	0.026	62.000	0.634	1.045	0.467	1.524	PUR-J
0.506	8.416	4.316	0.668	aqu	zoobenthos	0.026	62.000	0.028	2.042	0.405	1.452	PUR-O
0.532	17.189	6.196	1.020	aqu	zoobenthos	0.026	62.000	0.056	1.511	0.417	1.454	PUR-O
0.526	25.968	7.717	1.213	aqu	zoobenthos	0.026	62.000	0.085	1.362	0.435	1.345	PUR-O
0.560	35.359	9.078	1.360	aqu	zoobenthos	0.026	62.000	0.116	1.240	0.414	1.258	PUR-O
0.625	43.842	10.240	1.454	aqu	zoobenthos	0.026	62.000	0.144	1.214	0.352	1.149	PUR-O
0.732	53.234	11.561	1.527	aqu	zoobenthos	0.026	62.000	0.174	1.159	0.254	2.500	PUR-O
0.519	61.714	12.882	1.567	aqu	zoobenthos	0.026	62.000	0.202	1.142	0.465	1.247	PUR-O
0.577	70.506	13.804	1.631	aqu	zoobenthos	0.026	62.000	0.231	1.129	0.408	1.176	PUR-O
0.673	79.601	14.805	1.682	aqu	zoobenthos	0.026	62.000	0.261	1.110	0.315	2.208	PUR-O
0.454	88.390	15.887	1.716	aqu	zoobenthos	0.026	62.000	0.289	1.103	0.534	1.268	PUR-O
0.477	97.490	16.609	1.770	aqu	zoobenthos	0.026	62.000	0.319	1.093	0.512	1.014	PUR-O
0.641	106.591	17.331	1.816	aqu	zoobenthos	0.026	62.000	0.349	1.077	0.351	2.156	PUR-O
0.384	114.776	18.173	1.843	aqu	zoobenthos	0.026	62.000	0.376	1.077	0.608	1.180	PUR-O

0.432	123.577	18.695	1.889	aqu	zoobenthos	0.026	62.000	0.405	1.076	0.559	1.079	PUR-O
0.561	132.983	19.298	1.930	aqu	zoobenthos	0.026	62.000	0.436	1.064	0.431	1.546	PUR-O
0.492	141.477	19.980	1.957	aqu	zoobenthos	0.026	62.000	0.463	1.062	0.500	1.477	PUR-O
0.407	150.276	20.582	1.988	aqu	zoobenthos	0.026	62.000	0.492	1.059	0.586	1.362	PUR-O
0.329	159.078	21.064	2.022	aqu	zoobenthos	0.026	62.000	0.521	1.059	0.664	1.059	PUR-O
0.452	168.488	21.467	2.060	aqu	zoobenthos	0.026	62.000	0.552	1.050	0.542	1.337	PUR-O
0.425	176.986	21.949	2.087	aqu	zoobenthos	0.026	62.000	0.580	1.048	0.569	1.299	PUR-O
0.408	185.484	22.392	2.114	aqu	zoobenthos	0.026	62.000	0.608	1.049	0.586	1.280	PUR-O
0.395	194.591	22.834	2.143	aqu	zoobenthos	0.026	62.000	0.637	1.045	0.600	1.148	PUR-O
0.469	203.394	23.237	2.169	aqu	zoobenthos	0.026	62.000	0.666	1.045	0.525	1.502	PUR-O
0.603	9.947	4.676	0.755	aqu	zoobenthos	0.026	62.000	0.028	2.006	0.316	1.203	HAU-J
0.725	19.950	7.115	1.031	aqu	zoobenthos	0.026	62.000	0.055	1.519	0.235	2.521	HAU-J
0.542	30.310	9.634	1.146	aqu	zoobenthos	0.026	62.000	0.084	1.354	0.421	1.642	HAU-J
0.445	41.050	11.355	1.285	aqu	zoobenthos	0.026	62.000	0.114	1.244	0.528	1.283	HAU-J
0.465	51.084	12.516	1.406	aqu	zoobenthos	0.026	62.000	0.141	1.211	0.512	1.505	HAU-J
0.355	61.838	13.677	1.509	aqu	zoobenthos	0.026	62.000	0.171	1.174	0.626	1.157	HAU-J
0.416	72.600	14.479	1.612	aqu	zoobenthos	0.026	62.000	0.201	1.138	0.568	1.401	HAU-J
0.326	82.644	15.281	1.688	aqu	zoobenthos	0.026	62.000	0.229	1.126	0.661	1.228	HAU-J
0.305	93.052	15.883	1.768	aqu	zoobenthos	0.026	62.000	0.258	1.112	0.684	1.098	HAU-J
0.388	103.462	16.406	1.842	aqu	zoobenthos	0.026	62.000	0.286	1.104	0.600	1.324	HAU-J
0.331	114.229	17.048	1.902	aqu	zoobenthos	0.026	62.000	0.316	1.088	0.660	1.149	HAU-J
0.380	124.280	17.530	1.959	aqu	zoobenthos	0.026	62.000	0.344	1.087	0.610	1.202	HAU-J
0.412	135.048	18.093	2.010	aqu	zoobenthos	0.026	62.000	0.374	1.077	0.579	1.365	HAU-J
0.339	145.457	18.655	2.054	aqu	zoobenthos	0.026	62.000	0.403	1.072	0.653	1.156	HAU-J
0.386	155.869	19.098	2.099	aqu	zoobenthos	0.026	62.000	0.432	1.067	0.607	1.283	HAU-J
0.356	166.281	19.580	2.139	aqu	zoobenthos	0.026	62.000	0.460	1.065	0.637	1.299	HAU-J
0.289	177.052	20.023	2.180	aqu	zoobenthos	0.026	62.000	0.490	1.057	0.705	1.019	HAU-J
0.433	187.107	20.345	2.219	aqu	zoobenthos	0.026	62.000	0.518	1.056	0.561	1.335	HAU-J

0.396	197.518	20.828	2.250	aqu	zoobenthos	0.026	62.000	0.547	1.055	0.598	1.329	HAU-J
0.335	208.290	21.270	2.282	aqu	zoobenthos	0.026	62.000	0.577	1.052	0.659	1.037	HAU-J
0.475	219.063	21.633	2.315	aqu	zoobenthos	0.026	62.000	0.607	1.048	0.519	1.511	HAU-J
0.350	229.473	22.115	2.340	aqu	zoobenthos	0.026	62.000	0.635	1.042	0.645	1.199	HAU-J
0.364	239.169	22.438	2.366	aqu	zoobenthos	0.026	62.000	0.662	1.045	0.631	1.335	HAU-J
0.619	13.147	4.117	1.161	aqu	zoobenthos	0.026	62.000	0.029	1.935	0.306	2.104	HAU-S
0.474	25.444	6.196	1.413	aqu	zoobenthos	0.026	62.000	0.055	1.520	0.474	1.328	HAU-S
0.502	38.679	7.557	1.633	aqu	zoobenthos	0.026	62.000	0.084	1.366	0.459	1.256	HAU-S
0.569	52.832	8.839	1.788	aqu	zoobenthos	0.026	62.000	0.115	1.233	0.405	1.631	HAU-S
0.483	65.159	9.960	1.878	aqu	zoobenthos	0.026	62.000	0.142	1.210	0.493	1.470	HAU-S
0.412	78.865	10.922	1.977	aqu	zoobenthos	0.026	62.000	0.171	1.168	0.569	1.262	HAU-S
0.423	92.120	11.644	2.068	aqu	zoobenthos	0.026	62.000	0.200	1.144	0.560	1.215	HAU-S
0.470	105.377	12.326	2.146	aqu	zoobenthos	0.026	62.000	0.229	1.121	0.516	1.282	HAU-S
0.492	118.176	13.008	2.207	aqu	zoobenthos	0.026	62.000	0.257	1.116	0.494	1.664	HAU-S
0.292	131.889	13.730	2.262	aqu	zoobenthos	0.026	62.000	0.287	1.104	0.698	1.007	HAU-S
0.448	145.612	14.133	2.332	aqu	zoobenthos	0.026	62.000	0.316	1.091	0.542	1.397	HAU-S
0.383	158.873	14.695	2.381	aqu	zoobenthos	0.026	62.000	0.345	1.081	0.608	1.336	HAU-S
0.308	171.679	15.137	2.428	aqu	zoobenthos	0.026	62.000	0.373	1.080	0.684	1.017	HAU-S
0.459	185.404	15.500	2.482	aqu	zoobenthos	0.026	62.000	0.403	1.069	0.533	1.420	HAU-S
0.384	198.208	15.982	2.518	aqu	zoobenthos	0.026	62.000	0.431	1.067	0.608	1.368	HAU-S
0.281	211.474	16.385	2.558	aqu	zoobenthos	0.026	62.000	0.460	1.063	0.713	0.949	HAU-S
0.482	224.744	16.668	2.601	aqu	zoobenthos	0.026	62.000	0.488	1.061	0.511	1.557	HAU-S
0.333	238.465	17.150	2.632	aqu	zoobenthos	0.026	62.000	0.518	1.058	0.661	1.216	HAU-S
0.324	252.190	17.473	2.670	aqu	zoobenthos	0.026	62.000	0.548	1.051	0.671	1.262	HAU-S
0.261	265.002	17.756	2.703	aqu	zoobenthos	0.026	62.000	0.576	1.054	0.734	1.071	HAU-S
0.347	279.188	17.999	2.742	aqu	zoobenthos	0.026	62.000	0.607	1.046	0.648	1.363	HAU-S
0.206	291.999	18.281	2.771	aqu	zoobenthos	0.026	62.000	0.635	1.044	0.790	1.049	HAU-S
0.197	2992.127	9.156	5.789	aqu	zoobenthos	0.026	53.000	1.993	2.023	0.744	1.189	site 3

0.177	6054.420	10.520	6.355	aqu	zoobenthos	0.026	53.000	4.032	1.506	0.792	1.151	site 3
0.144	9115.616	11.310	6.692	aqu	zoobenthos	0.026	53.000	6.071	1.326	0.838	1.033	site 3
0.218	12091.301	11.780	6.934	aqu	zoobenthos	0.026	53.000	8.053	1.246	0.762	1.167	site 3
0.185	15066.942	12.360	7.106	aqu	zoobenthos	0.026	53.000	10.035	1.197	0.801	1.097	site 3
0.204	18042.492	12.780	7.253	aqu	zoobenthos	0.026	53.000	12.016	1.170	0.783	1.191	site 3
0.119	21103.028	13.195	7.377	aqu	zoobenthos	0.026	53.000	14.055	1.141	0.874	0.961	site 3
0.264	24078.127	13.404	7.494	aqu	zoobenthos	0.026	53.000	16.036	1.124	0.724	1.272	site 3
0.140	27053.528	13.823	7.579	aqu	zoobenthos	0.026	53.000	18.018	1.113	0.854	1.009	site 3
0.235	30113.613	14.031	7.671	aqu	zoobenthos	0.026	53.000	20.056	1.099	0.757	1.229	site 3
0.125	33089.013	14.344	7.744	aqu	zoobenthos	0.026	53.000	22.037	1.090	0.870	1.066	site 3
0.131	36063.963	14.500	7.819	aqu	zoobenthos	0.026	53.000	24.018	1.085	0.864	1.030	site 3
0.193	39123.898	14.656	7.890	aqu	zoobenthos	0.026	53.000	26.056	1.076	0.802	1.216	site 3
0.048	42098.998	14.864	7.949	aqu	zoobenthos	0.026	53.000	28.038	1.073	0.950	0.920	site 3
0.217	45158.783	14.915	8.016	aqu	zoobenthos	0.026	53.000	30.076	1.066	0.777	1.163	site 3
0.171	48133.882	15.123	8.066	aqu	zoobenthos	0.026	53.000	32.057	1.062	0.825	1.136	site 3
0.116	51108.832	15.279	8.115	aqu	zoobenthos	0.026	53.000	34.038	1.060	0.881	1.057	site 3
0.125	54168.767	15.382	8.167	aqu	zoobenthos	0.026	53.000	36.076	1.055	0.872	1.109	site 3
0.062	57143.717	15.485	8.213	aqu	zoobenthos	0.026	53.000	38.057	1.054	0.936	0.942	site 3
0.207	60203.502	15.535	8.262	aqu	zoobenthos	0.026	53.000	40.095	1.049	0.789	1.220	site 3
0.070	63178.452	15.691	8.301	aqu	zoobenthos	0.026	53.000	42.077	1.047	0.929	1.035	site 3
0.073	66153.251	15.741	8.343	aqu	zoobenthos	0.026	53.000	44.058	1.045	0.926	0.988	site 3
0.376	1582.204	8.945	5.175	aqu	zoobenthos	0.026	53.000	1.936	2.084	0.536	1.375	site 2
0.370	3296.870	11.790	5.633	aqu	zoobenthos	0.026	53.000	4.034	1.478	0.583	1.449	site 2
0.240	4871.719	13.625	5.879	aqu	zoobenthos	0.026	53.000	5.961	1.342	0.732	1.155	site 2
0.246	6538.212	14.623	6.103	aqu	zoobenthos	0.026	53.000	8.000	1.255	0.733	1.147	site 2
0.258	8204.558	15.463	6.274	aqu	zoobenthos	0.026	53.000	10.039	1.197	0.725	1.150	site 2
0.270	9824.465	16.198	6.408	aqu	zoobenthos	0.026	53.000	12.021	1.165	0.715	1.117	site 2
0.322	11444.372	16.880	6.519	aqu	zoobenthos	0.026	53.000	14.003	1.142	0.664	1.305	site 2

0.226	13064.361	17.614	6.609	aqu	zoobenthos	0.026	53.000	15.985	1.124	0.764	1.051	site 2
0.318	14684.022	18.086	6.699	aqu	zoobenthos	0.026	53.000	17.966	1.113	0.670	1.315	site 2
0.205	16350.189	18.715	6.773	aqu	zoobenthos	0.026	53.000	20.005	1.099	0.787	0.976	site 2
0.366	17969.769	19.081	6.848	aqu	zoobenthos	0.026	53.000	21.987	1.093	0.624	1.420	site 2
0.199	19635.853	19.711	6.904	aqu	zoobenthos	0.026	53.000	24.025	1.082	0.794	1.015	site 2
0.317	21255.352	20.024	6.967	aqu	zoobenthos	0.026	53.000	26.007	1.076	0.675	1.261	site 2
0.252	22875.095	20.496	7.018	aqu	zoobenthos	0.026	53.000	27.988	1.073	0.741	1.056	site 2
0.350	24540.935	20.862	7.070	aqu	zoobenthos	0.026	53.000	30.027	1.066	0.643	1.334	site 2
0.243	26160.596	21.333	7.112	aqu	zoobenthos	0.026	53.000	32.008	1.062	0.751	0.979	site 2
0.411	27780.094	21.647	7.157	aqu	zoobenthos	0.026	53.000	33.990	1.060	0.582	1.452	site 2
0.262	29446.097	22.171	7.192	aqu	zoobenthos	0.026	53.000	36.028	1.055	0.732	1.145	site 2
0.273	31065.596	22.485	7.231	aqu	zoobenthos	0.026	53.000	38.010	1.052	0.722	1.152	site 2
0.282	32685.175	22.798	7.268	aqu	zoobenthos	0.026	53.000	39.991	1.050	0.713	1.017	site 2
0.426	34304.674	23.112	7.303	aqu	zoobenthos	0.026	53.000	41.973	1.049	0.568	1.242	site 2
0.449	35970.595	23.584	7.330	aqu	zoobenthos	0.026	53.000	44.011	1.045	0.545	1.278	site 2
0.438	692.478	9.577	4.281	aqu	zoobenthos	0.026	53.000	1.937	2.084	0.472	1.391	site 1
0.462	1442.981	13.206	4.694	aqu	zoobenthos	0.026	53.000	4.036	1.492	0.488	1.362	site 1
0.467	2152.572	15.888	4.909	aqu	zoobenthos	0.026	53.000	6.020	1.330	0.497	1.441	site 1
0.414	2861.973	18.149	5.061	aqu	zoobenthos	0.026	53.000	8.004	1.255	0.559	1.195	site 1
0.476	3591.415	19.937	5.194	aqu	zoobenthos	0.026	53.000	10.044	1.197	0.501	1.492	site 1
0.385	4300.602	21.724	5.288	aqu	zoobenthos	0.026	53.000	12.028	1.165	0.597	1.186	site 1
0.435	5009.538	23.037	5.382	aqu	zoobenthos	0.026	53.000	14.010	1.142	0.548	1.301	site 1
0.431	5718.546	24.404	5.457	aqu	zoobenthos	0.026	53.000	15.993	1.124	0.555	1.293	site 1
0.428	6427.483	25.665	5.523	aqu	zoobenthos	0.026	53.000	17.976	1.113	0.559	1.360	site 1
0.376	7156.657	26.873	5.585	aqu	zoobenthos	0.026	53.000	20.015	1.102	0.613	1.227	site 1
0.387	7885.724	27.871	5.645	aqu	zoobenthos	0.026	53.000	22.054	1.090	0.602	1.193	site 1
0.430	8594.518	28.816	5.698	aqu	zoobenthos	0.026	53.000	24.037	1.082	0.561	1.430	site 1
0.323	9303.347	29.814	5.743	aqu	zoobenthos	0.026	53.000	26.019	1.078	0.669	1.225	site 1

	0.299	10032.307	30.548	5.794	aqu	zoobenthos	0.026	53.000	28.058	1.071	0.694	1.122	site 1
	0.355	10740.957	31.178	5.842	aqu	zoobenthos	0.026	53.000	30.040	1.068	0.638	1.344	site 1
	0.245	11469.917	31.912	5.884	aqu	zoobenthos	0.026	53.000	32.078	1.062	0.750	1.081	site 1
	0.312	12178.496	32.384	5.930	aqu	zoobenthos	0.026	53.000	34.060	1.058	0.682	1.244	site 1
	0.258	12887.146	32.961	5.969	aqu	zoobenthos	0.026	53.000	36.042	1.057	0.737	1.077	site 1
	0.337	13615.963	33.432	6.009	aqu	zoobenthos	0.026	53.000	38.080	1.052	0.657	1.230	site 1
	0.317	14324.613	34.009	6.043	aqu	zoobenthos	0.026	53.000	40.062	1.049	0.678	1.181	site 1
	0.327	15033.228	34.533	6.076	aqu	zoobenthos	0.026	53.000	42.044	1.047	0.668	1.233	site 1
	0.295	15741.842	35.057	6.107	aqu	zoobenthos	0.026	53.000	44.026	1.046	0.700	1.186	site 1
Condit R., Hubbeell S.P., Lafrankie J.V., Sukumar R., Manokaran N., Foster R.B. & Ashton P.S. (1996)	**0.526**	20.552	6.800	1.106	ter	plants	44000.000	11.600	400.000	1.563	0.419	1.392	Mudumalai
	0.481	32.113	8.600	1.317	ter	plants	44000.000	11.600	625.000	2.400	0.411	1.823	Mudumalai
	0.342	77.070	13.100	1.772	ter	plants	44000.000	11.600	1500.000	1.667	0.599	1.052	Mudumalai
	0.374	128.450	15.600	2.108	ter	plants	44000.000	11.600	2500.000	4.000	0.461	1.391	Mudumalai
	0.429	513.800	26.200	2.976	ter	plants	44000.000	11.600	10000.000	2.250	0.471	1.666	Mudumalai
	0.293	1156.050	37.100	3.439	ter	plants	44000.000	11.600	22500.000	1.778	0.646	1.238	Mudumalai
	0.287	2055.200	43.900	3.846	ter	plants	44000.000	11.600	40000.000	1.563	0.666	1.226	Mudumalai
	0.191	3211.250	49.900	4.164	ter	plants	44000.000	11.600	62500.000	4.000	0.690	1.315	Mudumalai
	0.509	195.272	53.700	1.291	ter	plants	44000.000	9.200	400.000	1.563	0.435	1.391	BCI
	0.457	305.113	67.400	1.510	ter	plants	44000.000	9.200	625.000	2.400	0.434	1.789	BCI
	0.309	732.270	100.600	1.985	ter	plants	44000.000	9.200	1500.000	1.667	0.635	1.153	BCI
	0.275	1220.450	117.800	2.338	ter	plants	44000.000	9.200	2500.000	4.000	0.578	1.480	BCI
	0.187	4881.800	172.400	3.343	ter	plants	44000.000	9.200	10000.000	2.250	0.747	1.194	BCI
	0.155	10984.050	200.600	4.003	ter	plants	44000.000	9.200	22500.000	1.778	0.805	1.132	BCI
	0.135	19527.200	219.300	4.489	ter	plants	44000.000	9.200	40000.000	1.563	0.838	1.044	BCI
	0.132	30511.250	232.900	4.875	ter	plants	44000.000	9.200	62500.000	4.000	0.778	1.178	BCI
	0.616	268.080	126.800	0.749	ter	plants	44000.000	3.000	400.000	1.563	0.333	1.579	Pasoh
	0.538	418.875	166.900	0.920	ter	plants	44000.000	3.000	625.000	2.400	0.356	2.037	Pasoh
	0.371	1005.300	267.300	1.325	ter	plants	44000.000	3.000	1500.000	1.667	0.569	1.229	Pasoh

	0.307	1675.500	323.000	1.646	ter	plants	44000.000	3.000	2500.000	4.000	0.538	1.571	Pasoh
	0.200	6702.000	494.500	2.607	ter	plants	44000.000	3.000	10000.000	2.250	0.731	1.223	Pasoh
	0.152	15079.500	581.400	3.256	ter	plants	44000.000	3.000	22500.000	1.778	0.808	1.107	Pasoh
	0.159	26808.000	634.600	3.743	ter	plants	44000.000	3.000	40000.000	1.563	0.809	1.120	Pasoh
	0.099	41887.500	681.400	4.119	ter	plants	44000.000	3.000	62500.000	4.000	0.828	1.153	Pasoh
Eggeling W.J. (1947)	**0.379**	117.167	10.087	2.452	ter	plants	44000.000	2.000	3699.040	2.014	0.537	1.331	ironwood
	0.396	235.984	13.157	2.887	ter	plants	44000.000	2.000	7450.180	1.492	0.556	1.146	ironwood
	0.527	141.029	39.502	1.273	ter	plants	44000.000	2.000	3764.670	1.998	0.388	1.558	swamp
	0.516	281.749	56.875	1.600	ter	plants	44000.000	2.000	7521.100	1.492	0.434	1.560	swamp
	0.379	149.443	21.691	1.930	ter	plants	44000.000	2.000	3730.710	2.013	0.538	1.425	colonizing
	0.334	300.852	28.269	2.365	ter	plants	44000.000	2.000	7510.510	1.489	0.621	1.271	colonizing
	0.422	171.134	32.756	1.653	ter	plants	44000.000	2.000	3734.800	2.020	0.492	1.500	mixed
	0.369	345.665	44.056	2.060	ter	plants	44000.000	2.000	7543.730	1.479	0.585	1.400	mixed
Kassas M. (1953)	**0.184**	11.300	2.987	1.331	ter	plants	10.000	30.000	24.688	4.274	0.694	0.542	kassas
	0.625	48.293	3.902	2.516	ter	plants	10.000	30.000	105.508	3.821	0.231	1.502	kassas
	0.713	184.537	9.022	3.018	ter	plants	10.000	30.000	403.164	2.227	0.210	2.557	kassas
	0.599	410.989	15.975	3.248	ter	plants	10.000	30.000	897.902	1.332	0.367	2.215	kassas
	0.290	547.439	18.965	3.363	ter	plants	10.000	30.000	1196.010	1.254	0.686	1.337	kassas
	0.133	686.366	20.253	3.523	ter	plants	10.000	30.000	1499.530	1.397	0.847	1.057	kassas
	0.030	1235.453	22.115	4.023	ter	plants	10.000	30.000	2699.140	1.111	0.968	0.921	kassas
	0.318	14.608	4.994	1.073	ter	plants	10.000	48.500	0.231	4.316	0.516	1.582	Gb
	0.192	63.044	7.954	2.070	ter	plants	10.000	48.500	0.995	4.012	0.689	1.181	Gb
	0.274	8.838	5.997	0.388	ter	plants	10.000	48.500	0.231	4.316	0.570	1.629	Gc
Pastor J., Downing A. & Erickson H.E. (1996)	**0.076**	38.145	8.958	1.449	ter	plants	10.000	48.500	0.995	4.012	0.866	0.763	Gc
	0.153	14.215	7.979	0.577	ter	plants	10.000	48.500	0.231	4.263	0.740	0.967	Ge
	0.289	60.602	9.961	1.806	ter	plants	10.000	48.500	0.983	4.074	0.557	1.694	Ge
	0.110	11.977	8.983	0.288	ter	plants	10.000	48.500	0.231	4.263	0.808	0.999	Gf
	0.199	51.060	10.530	1.579	ter	plants	10.000	48.500	0.983	4.062	0.677	1.113	Gf

	0.227	7.556	5.019	0.409	ter	plants	10.000	48.500	0.231	4.263	0.634	1.308	Sa
	0.177	32.214	6.976	1.530	ter	plants	10.000	48.500	0.983	4.099	0.707	1.275	Sa
	0.467	8.666	4.015	0.769	ter	plants	10.000	48.500	0.231	4.316	0.356	2.586	Sb
	0.086	37.399	7.954	1.548	ter	plants	10.000	48.500	0.995	4.012	0.851	1.064	Sb
	0.125	9.854	4.994	0.680	ter	plants	10.000	48.500	0.231	4.316	0.782	0.660	Sc
	0.484	42.527	5.997	1.959	ter	plants	10.000	48.500	0.995	4.024	0.348	1.791	Sc
	0.273	13.117	7.979	0.497	ter	plants	10.000	48.500	0.243	4.150	0.576	1.448	Sd
	0.172	54.437	11.760	1.532	ter	plants	10.000	48.500	1.007	3.988	0.717	1.313	Sd
	0.402	9.923	4.994	0.687	ter	plants	10.000	48.500	0.231	4.316	0.422	1.795	Se
	0.249	42.826	8.983	1.562	ter	plants	10.000	48.500	0.995	4.037	0.609	1.281	Se
	0.745	8.642	3.012	1.054	ter	plants	10.000	48.500	0.231	4.316	0.136	5.551	Sf
	0.252	37.298	8.958	1.426	ter	plants	10.000	48.500	0.995	4.024	0.606	1.513	Sf
	0.611	77.580	56.884	0.310	ter	plants	44000.000	2.000	1746.883	2.402	0.290	1.988	poore
	0.525	186.347	97.159	0.651	ter	plants	44000.000	2.000	4196.031	1.772	0.405	1.351	poore
	0.576	330.201	131.177	0.923	ter	plants	44000.000	2.000	7435.227	1.492	0.376	1.572	poore
	0.426	134.354	22.858	1.771	ter	plants	44000.000	7.000	3715.587	1.998	0.488	1.616	sp4
	0.304	268.461	30.703	2.168	ter	plants	44000.000	7.000	7424.330	1.498	0.652	1.244	sp4
	0.425	196.289	25.964	2.023	ter	plants	44000.000	7.000	3722.252	1.997	0.489	1.570	sp2
	0.330	391.982	34.845	2.420	ter	plants	44000.000	7.000	7433.217	1.495	0.624	1.252	sp2
Poore M.E.D. (1964)	**0.536**	147.080	36.008	1.407	ter	plants	44000.000	6.300	3743.802	1.988	0.380	1.715	sp3
	0.465	292.458	52.034	1.726	ter	plants	44000.000	6.300	7444.281	1.503	0.484	1.550	sp3
	0.772	9.615	3.560	0.993	ter	plants	10.000	20.000	4.356	2.258	0.162	3.035	heath
Richards P.W. (1939)	**0.599**	21.708	6.677	1.179	ter	plants	10.000	20.000	9.833	1.896	0.326	2.462	heath
	0.258	41.160	9.794	1.436	ter	plants	10.000	20.000	18.644	2.011	0.672	1.007	heath
	0.399	82.753	11.730	1.954	ter	plants	10.000	20.000	37.485	2.094	0.511	1.544	heath
	0.303	173.291	15.752	2.398	ter	plants	10.000	20.000	78.495	1.509	0.652	1.400	heath
	0.130	261.481	17.845	2.685	ter	plants	10.000	20.000	118.443	1.666	0.840	0.786	heath
	0.391	435.573	19.066	3.129	ter	plants	10.000	20.000	197.302	2.626	0.492	1.868	heath

Vaughan R.E. & Wiehe P.O. (1941)	**0.795**	5.722	5.191	0.097	ter	plants	10.000	20.000	3.204	2.348	0.142	4.002	upland
	0.501	13.436	10.234	0.272	ter	plants	10.000	20.000	7.522	2.312	0.396	1.657	upland
	0.416	31.059	15.576	0.690	ter	plants	10.000	20.000	17.389	2.203	0.487	1.474	upland
	0.356	68.420	21.629	1.152	ter	plants	10.000	20.000	38.306	2.039	0.561	1.375	upland
	0.326	139.508	27.864	1.611	ter	plants	10.000	20.000	78.106	1.510	0.627	1.198	upland
	0.339	210.695	31.879	1.888	ter	plants	10.000	20.000	117.961	1.676	0.602	1.077	upland
	0.404	353.156	37.983	2.230	ter	plants	10.000	20.000	197.720	2.620	0.479	1.542	upland
	0.559	28.492	13.770	0.727	ter	plants	10.000	20.000	7.425	2.464	0.333	1.363	sideroxylon
	0.635	70.215	22.805	1.125	ter	plants	10.000	20.000	18.299	1.894	0.294	2.385	sideroxylon
	0.365	133.004	34.210	1.358	ter	plants	10.000	20.000	34.662	2.240	0.539	1.406	sideroxylon
	0.342	297.974	45.923	1.870	ter	plants	10.000	20.000	77.655	1.512	0.611	1.316	sideroxylon
	0.275	450.620	52.898	2.142	ter	plants	10.000	20.000	117.436	1.688	0.672	1.280	sideroxylon
	0.171	760.728	61.075	2.522	ter	plants	10.000	20.000	198.253	2.617	0.754	1.174	sideroxylon
	0.003	26.321	3.990	1.886	ter	plants	10.000	45.000	0.248	4.054	0.995	0.247	andrew high
	0.811	106.708	4.007	3.282	ter	plants	10.000	45.000	1.007	1.998	0.140	5.058	andrew high
	0.369	213.190	7.022	3.413	ter	plants	10.000	45.000	2.011	1.996	0.549	1.574	andrew high
	0.175	425.624	9.060	3.850	ter	plants	10.000	45.000	4.016	2.262	0.762	0.597	andrew high
	0.160	2110.574	16.958	4.824	ter	plants	10.000	45.000	19.913	2.014	0.790	0.992	andrew high
	0.284	4250.720	18.964	5.412	ter	plants	10.000	45.000	40.104	1.978	0.644	1.181	andrew high
	0.137	15.106	6.997	0.770	ter	plants	10.000	45.000	0.246	6.131	0.736	0.983	andrew interm.
Weiher E. (1999)	**0.469**	244.156	12.270	2.991	aqu	plants	10.000	45.000	3.983	1.997	0.445	0.941	andrew interm.
	0.711	487.463	16.969	3.358	aqu	plants	10.000	45.000	7.951	1.267	0.265	3.233	andrew interm.
	0.194	617.653	20.080	3.426	aqu	plants	10.000	45.000	10.075	1.978	0.749	1.208	andrew interm.
	0.131	1221.611	22.920	3.976	aqu	plants	10.000	45.000	19.927	2.014	0.827	1.121	andrew interm.
	0.103	2460.209	25.113	4.585	aqu	plants	10.000	45.000	40.131	1.996	0.863	0.974	andrew interm.
	0.193	11.453	9.852	0.151	aqu	plants	10.000	45.000	0.249	4.020	0.687	1.020	andrew low
	0.378	46.041	12.880	1.274	aqu	plants	10.000	45.000	1.000	1.997	0.539	1.695	andrew low
	0.102	91.922	16.729	1.704	aqu	plants	10.000	45.000	1.997	2.998	0.841	1.097	andrew low

0.067	467.925	19.876	3.159	aqu	plants	10.000	45.000	10.167	1.977	0.910	0.943	andrew low
0.191	925.278	20.800	3.795	aqu	plants	10.000	45.000	20.104	1.996	0.752	1.268	andrew low
0.067	1846.750	23.741	4.354	aqu	plants	10.000	45.000	40.126	1.977	0.910	0.865	andrew low
0.242	11.622	9.033	0.252	aqu	plants	10.000	45.000	0.248	3.977	0.620	1.060	lucerne blvd
0.426	46.224	12.620	1.298	aqu	plants	10.000	45.000	0.985	1.986	0.490	1.926	lucerne blvd
0.079	91.782	16.901	1.692	aqu	plants	10.000	45.000	1.956	2.021	0.893	0.993	lucerne blvd
0.156	185.511	17.868	2.340	aqu	plants	10.000	45.000	3.954	1.985	0.796	0.708	lucerne blvd
0.579	368.212	19.880	2.919	aqu	plants	10.000	45.000	7.849	1.269	0.392	2.319	lucerne blvd
0.124	467.104	22.815	3.019	aqu	plants	10.000	45.000	9.957	2.003	0.835	0.957	lucerne blvd
0.264	935.598	24.871	3.627	aqu	plants	10.000	45.000	19.943	2.003	0.666	1.359	lucerne blvd
0.132	1874.415	29.874	4.139	aqu	plants	10.000	45.000	39.955	2.003	0.826	1.092	lucerne blvd
0.086	21.651	15.281	0.348	aqu	plants	10.000	45.000	0.254	4.012	0.850	1.166	luskville high
0.013	86.870	17.219	1.618	aqu	plants	10.000	45.000	1.021	2.012	0.982	0.838	luskville high
0.236	174.758	17.376	2.308	aqu	plants	10.000	45.000	2.053	1.977	0.699	1.246	luskville high
0.167	345.485	20.410	2.829	aqu	plants	10.000	45.000	4.059	2.249	0.772	1.101	luskville high
0.050	1725.006	27.307	4.146	aqu	plants	10.000	45.000	20.265	1.994	0.932	0.768	luskville high
0.362	3439.278	28.263	4.801	aqu	plants	10.000	45.000	40.405	1.978	0.557	1.430	luskville high
0.093	9.701	7.082	0.315	aqu	plants	10.000	45.000	0.251	4.049	0.839	0.888	luskville interm.
0.328	39.279	8.061	1.584	aqu	plants	10.000	45.000	1.017	1.996	0.593	1.509	luskville interm.
0.143	78.386	10.112	2.048	aqu	plants	10.000	45.000	2.029	2.013	0.811	1.123	luskville interm.
0.125	157.758	11.177	2.647	aqu	plants	10.000	45.000	4.084	1.976	0.835	0.895	luskville interm.
0.377	311.766	12.169	3.243	aqu	plants	10.000	45.000	8.071	1.255	0.596	1.426	luskville interm.
0.201	391.342	13.258	3.385	aqu	plants	10.000	45.000	10.131	2.013	0.739	0.892	luskville interm.
0.423	787.761	15.260	3.944	aqu	plants	10.000	45.000	20.394	1.996	0.492	1.547	luskville interm.
0.310	1572.528	20.445	4.343	aqu	plants	10.000	45.000	40.711	1.977	0.614	1.432	luskville interm.
0.299	18.721	9.010	0.731	aqu	plants	10.000	45.000	1.017	1.995	0.626	1.020	luskville low
0.445	37.356	11.076	1.216	aqu	plants	10.000	45.000	2.030	1.996	0.469	2.100	luskville low
0.021	74.575	15.066	1.599	aqu	plants	10.000	45.000	4.053	1.976	0.971	0.878	luskville low

0.234	147.329	15.281	2.266	aqu	plants	10.000	45.000	8.007	1.267	0.744	1.213	luskville low
0.115	186.595	16.150	2.447	aqu	plants	10.000	45.000	10.141	2.976	0.822	1.058	luskville low
0.456	12.642	8.065	0.449	aqu	plants	10.000	45.000	0.251	3.964	0.377	2.266	westmeath high
0.198	50.111	15.108	1.199	aqu	plants	10.000	45.000	0.996	1.989	0.744	1.269	westmeath high
0.078	99.683	17.311	1.751	aqu	plants	10.000	45.000	1.980	2.025	0.895	0.897	westmeath high
0.249	201.884	18.286	2.402	aqu	plants	10.000	45.000	4.011	2.248	0.670	1.379	westmeath high
0.235	1004.556	24.244	3.724	aqu	plants	10.000	45.000	19.958	1.990	0.700	1.303	westmeath high
0.121	1998.568	28.494	4.251	aqu	plants	10.000	45.000	39.707	2.026	0.839	0.899	westmeath high
0.123	20.447	14.143	0.369	aqu	plants	10.000	45.000	0.986	3.027	0.810	0.993	westmeath interm
0.169	162.403	20.324	2.078	aqu	plants	10.000	45.000	7.833	1.269	0.814	1.160	westmeath interm
0.079	206.123	21.160	2.276	aqu	plants	10.000	45.000	9.941	2.007	0.894	1.074	westmeath interm
0.057	413.646	22.352	2.918	aqu	plants	10.000	45.000	19.950	2.007	0.923	0.958	westmeath interm
0.159	830.037	23.255	3.575	aqu	plants	10.000	45.000	40.033	2.007	0.791	1.167	westmeath interm
0.063	25.139	18.231	0.321	aqu	plants	10.000	45.000	1.981	2.007	0.915	1.084	westmeath low
0.011	50.449	19.045	0.974	aqu	plants	10.000	45.000	3.975	2.264	0.984	0.875	westmeath low
0.109	257.866	22.239	2.451	aqu	plants	10.000	45.000	20.319	1.989	0.854	1.166	westmeath low
0.006	512.813	23.974	3.063	aqu	plants	10.000	45.000	40.408	2.006	0.992	0.781	westmeath low
0.297	6.662	4.304	0.437	aqu	plants	0.026	42.500	0.038	2.082	0.623	1.266	sample 3
0.304	13.872	5.352	0.952	aqu	plants	0.026	42.500	0.079	1.506	0.651	1.237	sample 3
0.295	20.896	6.063	1.237	aqu	plants	0.026	42.500	0.120	1.332	0.674	1.179	sample 3
0.315	27.828	6.598	1.439	aqu	plants	0.026	42.500	0.159	1.252	0.660	1.253	sample 3
0.276	34.848	7.083	1.593	aqu	plants	0.026	42.500	0.200	1.204	0.705	1.259	sample 3
0.190	41.953	7.455	1.728	aqu	plants	0.026	42.500	0.240	1.167	0.798	1.188	sample 3
0.094	48.967	7.678	1.853	aqu	plants	0.026	42.500	0.280	1.143	0.900	0.972	sample 3
0.212	55.978	7.775	1.974	aqu	plants	0.026	42.500	0.320	1.125	0.778	1.278	sample 3
0.325	18.783	4.592	1.409	aqu	plants	0.026	42.500	0.039	2.041	0.594	1.455	sample 22
0.205	38.331	5.790	1.890	aqu	plants	0.026	42.500	0.080	1.496	0.761	1.188	sample 22
0.155	57.348	6.288	2.210	aqu	plants	0.026	42.500	0.120	1.331	0.826	1.136	sample 22

	0.106	76.352	6.573	2.452	aqu	plants	0.026	42.500	0.159	1.255	0.883	1.074	sample 22
	0.089	95.835	6.732	2.656	aqu	plants	0.026	42.500	0.200	1.198	0.903	1.088	sample 22
	0.032	114.828	6.842	2.820	aqu	plants	0.026	42.500	0.240	1.170	0.966	1.015	sample 22
	0.037	134.304	6.876	2.972	aqu	plants	0.026	42.500	0.280	1.143	0.960	1.000	sample 22
	0.073	153.536	6.911	3.101	aqu	plants	0.026	42.500	0.320	1.125	0.923	1.076	sample 22
	0.442	27.187	5.195	1.655	aqu	plants	0.026	42.500	0.249	2.003	0.473	1.543	sample 13
	0.377	54.463	7.061	2.043	aqu	plants	0.026	42.500	0.498	1.510	0.573	1.386	sample 13
	0.310	82.257	8.250	2.300	aqu	plants	0.026	42.500	0.752	1.331	0.659	1.254	sample 13
	0.273	109.472	9.013	2.497	aqu	plants	0.026	42.500	1.001	1.248	0.704	1.220	sample 13
	0.231	136.675	9.577	2.658	aqu	plants	0.026	42.500	1.250	1.201	0.753	1.171	sample 13
	0.199	164.148	9.990	2.799	aqu	plants	0.026	42.500	1.501	1.167	0.788	1.128	sample 13
	0.190	191.615	10.303	2.923	aqu	plants	0.026	42.500	1.752	1.142	0.800	1.132	sample 13
Weinberg S. (1978)	**0.165**	218.802	10.566	3.031	aqu	zoobenthos	0.026	42.500	2.001	1.128	0.826	1.096	sample 13
	0.453	16.456	7.499	0.786	aqu	zoobenthos	0.026	42.500	0.250	2.000	0.461	1.714	sample 27
	0.303	32.919	10.265	1.165	aqu	zoobenthos	0.026	42.500	0.500	1.499	0.653	1.302	sample 27
	0.234	49.333	11.605	1.447	aqu	zoobenthos	0.026	42.500	0.749	1.336	0.739	1.196	sample 27
	0.189	65.897	12.419	1.669	aqu	zoobenthos	0.026	42.500	1.000	1.251	0.793	1.181	sample 27
	0.110	82.452	12.957	1.851	aqu	zoobenthos	0.026	42.500	1.252	1.201	0.881	1.052	sample 27
	0.127	98.997	13.220	2.013	aqu	zoobenthos	0.026	42.500	1.503	1.167	0.864	1.081	sample 27
	0.117	115.542	13.482	2.148	aqu	zoobenthos	0.026	42.500	1.754	1.143	0.876	1.078	sample 27
	0.100	132.086	13.695	2.266	aqu	zoobenthos	0.026	42.500	2.005	1.125	0.895	1.081	sample 27
	0.347	39.483	10.879	1.289	aqu	zoobenthos	0.026	42.500	0.249	2.004	0.572	1.527	sample 10
	0.191	79.126	13.846	1.743	aqu	zoobenthos	0.026	42.500	0.499	1.499	0.776	1.197	sample 10
	0.116	118.618	14.960	2.071	aqu	zoobenthos	0.026	42.500	0.748	1.336	0.868	1.072	sample 10
	0.117	158.463	15.473	2.326	aqu	zoobenthos	0.026	42.500	0.999	1.251	0.871	1.095	sample 10
	0.082	198.299	15.886	2.524	aqu	zoobenthos	0.026	42.500	1.251	1.199	0.911	1.033	sample 10
	0.104	237.720	16.124	2.691	aqu	zoobenthos	0.026	42.500	1.499	1.168	0.888	1.080	sample 10
	0.074	277.545	16.387	2.829	aqu	zoobenthos	0.026	42.500	1.750	1.143	0.922	1.028	sample 10

	0.095	317.361	16.550	2.954	aqu	zoobenthos	0.026	42.500	2.001	1.125	0.899	1.038	sample 10
	0.297	6978.562	101.601	4.230	aqu	zoobenthos	450.000	49.000	130913.784	4.051	0.548	1.576	region 1
	0.177	28272.420	139.270	5.313	aqu	zoobenthos	450.000	49.000	530374.251	2.228	0.761	1.189	region 1
	0.139	63000.782	153.985	6.014	aqu	zoobenthos	450.000	49.000	1181858.231	1.777	0.825	1.094	region 1
	0.148	111964.051	160.450	6.548	aqu	zoobenthos	450.000	49.000	2100380.830	1.574	0.822	1.127	region 1
	0.116	176197.899	166.760	6.963	aqu	zoobenthos	450.000	49.000	3305370.670	1.451	0.864	1.095	region 1
	0.089	255725.292	171.569	7.307	aqu	zoobenthos	450.000	49.000	4797258.547	1.350	0.898	1.055	region 1
	0.089	345103.675	174.127	7.592	aqu	zoobenthos	450.000	49.000	6473945.308	1.296	0.900	1.051	region 1
	0.091	447237.800	176.233	7.839	aqu	zoobenthos	450.000	49.000	8389922.423	1.296	0.898	1.039	region 1
	0.117	579606.999	178.191	8.087	aqu	zoobenthos	450.000	49.000	10873092.015	1.195	0.873	1.041	region 1
	0.330	7276.304	99.353	4.294	aqu	zoobenthos	450.000	49.000	132007.765	4.016	0.510	1.682	region 2
	0.185	29225.194	142.567	5.323	aqu	zoobenthos	450.000	49.000	530207.724	2.228	0.750	1.219	region 2
	0.125	65123.894	157.283	6.026	aqu	zoobenthos	450.000	49.000	1181487.151	1.791	0.841	1.110	region 2
	0.102	116661.068	165.396	6.559	aqu	zoobenthos	450.000	49.000	2116482.052	1.574	0.876	1.051	region 2
	0.126	183634.154	169.158	6.990	aqu	zoobenthos	450.000	49.000	3331517.498	1.440	0.853	1.081	region 2
	0.129	264384.685	173.217	7.331	aqu	zoobenthos	450.000	49.000	4796505.366	1.338	0.855	1.104	region 2
	0.094	353863.107	177.124	7.600	aqu	zoobenthos	450.000	49.000	6419835.904	1.317	0.893	0.935	region 2
	0.261	466059.796	179.831	7.860	aqu	zoobenthos	450.000	49.000	8455324.534	1.255	0.717	1.145	region 2
	0.282	584725.853	181.787	8.076	aqu	zoobenthos	450.000	49.000	10608181.368	1.234	0.696	1.303	region 2
	0.250	7206.328	109.845	4.184	aqu	zoobenthos	450.000	49.000	132949.484	4.020	0.609	1.470	region 3
	0.137	28970.590	143.467	5.308	aqu	zoobenthos	450.000	49.000	534478.170	2.247	0.811	1.147	region 3
	0.103	65098.800	155.485	6.037	aqu	zoobenthos	450.000	49.000	1201007.237	1.763	0.869	1.066	region 3
	0.113	114776.433	160.300	6.574	aqu	zoobenthos	450.000	49.000	2117509.468	1.574	0.863	1.069	region 3
	0.122	180654.688	164.811	7.000	aqu	zoobenthos	450.000	49.000	3332896.858	1.451	0.857	1.035	region 3
Storch D., Šizling A.L. & Gaston K.J. (2003)	**0.181**	262216.120	168.721	7.349	ter	birds	450.000	49.000	4837623.051	1.328	0.798	1.137	region 3
	0.152	348131.613	172.477	7.610	ter	birds	450.000	49.000	6422677.285	1.317	0.830	1.091	region 3
	0.157	458406.355	177.583	7.856	ter	birds	450.000	49.000	8457135.106	1.275	0.826	1.052	region 3
	0.214	584508.886	179.839	8.086	ter	birds	450.000	49.000	10783599.672	1.224	0.769	1.164	region 3

	0.129	1789139.899	156.824	9.342	ter	birds	450.000	49.000	2539112.885	3.972	0.783	1.179	central European
	0.102	7106874.173	178.191	10.594	ter	birds	450.000	49.000	10085938.945	2.269	0.857	1.081	central European
	0.109	16125055.868	187.301	11.363	ter	birds	450.000	49.000	22884368.713	1.764	0.862	1.084	central European
	0.103	28452025.694	193.724	11.897	ter	birds	450.000	49.000	40378566.868	1.550	0.875	1.085	central European
	0.081	44092890.969	199.251	12.307	ter	birds	450.000	49.000	62575781.616	1.441	0.905	1.060	central European
	0.069	63517068.552	202.685	12.655	ter	birds	450.000	49.000	90142200.324	1.361	0.921	1.060	central European
	0.040	86446189.060	205.223	12.951	ter	birds	450.000	49.000	122682766.525	1.307	0.954	1.039	central European
	0.015	112974425.205	207.013	13.210	ter	birds	450.000	49.000	160331128.318	1.265	0.983	1.010	central European
	0.014	142922971.190	207.458	13.443	ter	birds	450.000	49.000	202833527.959	1.235	0.985	1.009	central European
	0.011	176464544.751	207.754	13.652	ter	birds	450.000	49.000	250435083.132	1.215	0.988	1.007	central European
	0.009	214373271.660	208.050	13.845	ter	birds	450.000	49.000	304234418.223	1.176	0.991	1.005	central European
	0.009	252113566.534	208.197	14.007	ter	birds	450.000	49.000	357794717.816	1.176	0.991	1.004	central European
	0.009	296498019.265	208.344	14.168	ter	birds	450.000	49.000	420784278.269	1.167	0.990	0.996	central European